

CORN AND CORN IMPROVEMENT

AGRONOMY

A Series of Monographs Prepared under the Auspices of
THE AMERICAN SOCIETY OF AGRONOMY

General Editor

A. G. NORMAN

CHAIRMAN, COMMITTEE ON MONOGRAPHS

- I. C. EDMUND MARSHALL: The Colloid Chemistry of the Silicate Minerals, 1949
- II. BYRON T. SHAW, Editor: Soil Physical Conditions and Plant Growth, 1952
- III. K. D. JACOB, Editor: Fertilizer Technology and Resources in the United States, 1953
- IV. W. H. PIERRE and A. G. NORMAN, Editors: Soil and Fertilizer Phosphorus in Corn Nutrition, 1953
- V. GEORGE F. SPRAGUE, Editor: Corn and Corn Improvement, 1955

CORN

and

CORN IMPROVEMENT

Edited by

GEORGE F. SPRAGUE

*Agricultural Research Service,
U. S. Department of Agriculture and
Department of Agronomy,
Iowa State College, Ames, Iowa*



ACADEMIC PRESS INC., PUBLISHERS

NEW YORK, N. Y.

1955

✓

CHECKED

633.15

SP 72 C

COPYRIGHT, 1955 BY
ACADEMIC PRESS INC.

125 East 23rd Street
New York 10, N. Y.

All Rights Reserved

NO PART OF THIS BOOK MAY BE REPRODUCED IN
ANY FORM, BY PHOTOSTAT, MICROFILM, OR ANY
OTHER MEANS, WITHOUT WRITTEN PERMISSION
FROM THE PUBLISHERS.

ALLAMA IQBAL LIBRARY
53743

Library of Congress Catalog Card No. 55-8262

ST 01
R61

J. O. R.	53743
Acc.	16.3.65
Date	

88

CONTRIBUTORS

JOHN AIRY, *Pioneer Hybrid Corn Company, Johnston, Iowa*

ARTHUR M. BRUNSON,* *Department of Botany, Purdue Agricultural Experiment Station, Lafayette, Indiana*

F. F. DICKE,* *Federal Corn Borer Laboratory, Ankeny, Iowa*

L. F. RANDOLPH, *Department of Botany, Cornell University, Ithaca, New York*

M. M. RHOADES, *Department of Botany, University of Illinois, Urbana, Illinois*

JOHN E. SASS, *Department of Botany and Plant Physiology, Iowa State College, Ames, Iowa*

J. D. SAYRE,* *Ohio Agricultural Experiment Station, Wooster, Ohio*

BURCH N. SCHNEIDER,* *Department of Animal Husbandry, Washington State College, Pullman, Washington*

ROBERT H. SHAW, *Department of Agronomy, Iowa State College, Ames, Iowa*

GLENN M. SMITH,* *Department of Botany, Purdue Agricultural Experiment Station, Lafayette, Indiana*

GEORGE F. SPRAGUE,* *Department of Agronomy, Iowa State College, Ames, Iowa*

G. H. STRINGFIELD,* *Ohio Agricultural Experiment Station, Wooster, Ohio*

ARNOLD J. ULLSTRUP,* *Department of Botany, Purdue Agricultural Experiment Station, Lafayette, Indiana*

PAUL WEATHERWAX, *Department of Botany, University of Indiana, Bloomington, Indiana*

* *Agricultural Research Service, U.S. Department of Agriculture.*

PREFACE

Corn was indigenous in the Americas at the time of their discovery. Its production and utilization played an important role in successful colonization. In fact one historian has stated "The maize plant was the bridge over which English civilization crept, tremblingly and uncertainly, at first, then boldly and surely to a foothold and permanent occupation of America."

Tremendous developments have been made in agricultural methods since the first colonization, and throughout this whole period corn has remained one of the major crops grown in the New World. In the beginning the only corn available was the type or types being grown by the natives. Although the early history of corn domestication is still largely shrouded in mystery, by 1800 a large number of varieties were in existence. Through the efforts of private and public agencies intensive work was done on mass selection followed in order by varietal hybridization and ear-to-row breeding. Finally the present method of inbreeding and hybridization emerged from the early studies of Shull, East, Jones, and others. This present method is continuing to show progress as evidenced by the rapid replacement of the first commercial hybrids by newer and better combinations. The limits of further improvement are not yet definable by corn breeders.

Concomitant with the development of improvements in breeding methods has been the acquisition of increased knowledge of plant morphology, of mode of pollination, and most recently of the genetics and cytology of corn. At the present time more is known concerning the genetics and cytology of the corn plant than of any other plant species.

Although the most spectacular improvement in corn yields have come from plant breeding, marked progress also has been made in production practices. Fertilization of the crop has changed from the use of one or two fish per hill in certain restricted areas to the extensive use of balanced starter and supplemental commercial fertilizers. Production practices also have changed from a laborious hand culture to a high degree of mechanization.

Utilization has evolved from the various types of hand grinding used by the Indians through the water powered grist mill to present day types of milling which produce a bewildering array of products and by-products. Even the use of corn as a feed has undergone change; from reliance on exclusive use of corn in a fattening ration, practices have become diverse through adoption of extensive supplementation and have resulted in decreasing by at least one half the pounds of feed required per 100 pounds of gain.

Obviously the present Monograph cannot hope to cover all of these developments in any detail. In fact many of them will be largely ignored, and emphasis will be placed primarily upon the present status of our knowledge. Even with this limitation the preparation of this Monograph has posed many problems. It has been assumed that the particular agronomic audience to be served is the research worker and advanced student interested in corn. Even within this limited group interests are so varied that no choice of topics could be universally satisfactory.

The subject matter covered in the Monograph may be divided in three broad divisions; breeding, production, and utilization. Under the broad classification of breeding are included such topics as history and origin, morphology, cytogenetics, and breeding. The chapters included under the general topic of production treat with climatic requirements, mineral nutrition, culture, production of hybrid seed, the special crops, sweet corn and popcorn, and diseases and insect pests. Utilization is treated under the headings of industrial utilization and corn as a livestock feed.

Any bias which is apparent in the choice of the various sub-topics and in the relative space assigned is to be charged primarily to the editor although some contributors did not use all of the space and others exceeded the space allocations originally made. In any volume involving multiple authorship it is extremely difficult to obtain uniformity of treatment among chapters. This is particularly true where all coordination must be done by correspondence. Certainly others serving in an editorial capacity might well have chosen a somewhat different array of topics and made quite different space allocations than were used here.

The volume includes a rather large number of illustrations. The general policy was followed of using adequate illustrations where this was felt to be an essential part of the presentation, and limiting illustration in other chapters where they did not serve an equally important function.

The editor wishes to express his sincere appreciation to the authors of the several chapters who were persuaded to take the necessary time, often against their better judgment, from their already full research and teaching schedules to prepare their separate contributions.

G. F. SPRAGUE

Ames, Iowa
May, 1955

CONTENTS

	<i>Page</i>
CONTRIBUTORS	v
PREFACE	vii
I. <u>History and Origin of Corn</u>	
PAUL WEATHERWAX and L. F. RANDOLPH	
I. Early History of Corn and Theories as to Its Origin. PAUL WEATHERWAX.	1
II. Cytogenetic Aspects of the Origin and Evolutionary History of Corn. L. F. RANDOLPH.....	16
References.....	57
II. <u>Vegetative Morphology</u>	
JOHN E. SASS	
I. Development of the Caryopsis.....	63
II. Histology of the Vegetative Plant Body.....	75
References	87
III. <u>Structure and Development of Reproductive Organs</u>	
PAUL WEATHERWAX	
I. Introduction	89
II. The Spikelet and Flower.....	89
III. The Inflorescences.....	90
IV. Development of Flower and Inflorescence.....	97
V. Gametophytes and Fertilization.....	103
VI. Other Maydeae.....	105
VII. Floral Abnormalities in Corn.....	110
VIII. Anomalous Ears.....	115
References	119
IV. <u>The Cytogenetics of Maize</u>	
M. M. RHOADES	
I. Introduction	123
II. Chromosome Morphology.....	124
III. Polyploidy	131
IV. B Chromosomes.....	138
V. Meiosis in Maize.....	139
VI. Crossing Over in Maize.....	147
VII. Translocations	169
VIII. Inversions	183
IX. Deficiencies	192
X. Ring Chromosomes.....	195
XI. Abnormal Chromosome 10.....	197
XII. Mutation	201
References	212

V. Corn Breeding~~G. F. SPRAGUE~~

I. Introduction	221
II. Mass Selection.....	221
III. Varietal Hybridization.....	225
IV. Ear-to-Row Selection.....	228
V. Selection within and among Inbred Lines.....	233
VI. Evaluation of Inbred Lines.....	245
VII. The Prediction of Double-Cross Performance.....	251
VIII. Multiple Hybrids and Synthetics.....	254
IX. Recurrent Selection.....	257
X. Types of Gene Action.....	263
XI. Cytoplasmic Sterility.....	269
XII. Insect Resistance.....	272
XIII. Disease Resistance.....	275
XIV. Chemical Composition.....	279
XV. Conclusion	282
References.....	283

VI. Mineral Nutrition of Corn~~J. D. SAYRE~~

I. Introduction	293
II. Growth and Development of the Corn Plant.....	294
III. Percentage Composition of the Tissues.....	294
IV. Accumulation by the Whole Plant.....	298
V. Mineral Accumulation in Corn Leaves.....	301
VI. Summary	312
References.....	313

VII. Climatic Requirement

ROBERT H. SHAW

I. Introduction	315
II. World-Wide Corn Production and Climate.....	315
III. Climatic Regions of Corn Production.....	316
IV. Effect of Weather on Certain Periods of Plant Growth.....	318
V. Effect of Rainfall and Temperature on Yield.....	325
VI. Other Weather Factors.....	335
VII. Concluding Remarks.....	338
References.....	339

VIII. Corn Culture

G. H. STRINGFIELD

I. Introduction	343
II. Soil Requirements.....	344
III. First Preparations.....	345
IV. Lime and Fertilizers.....	349
V. Final Preparations and Planting.....	355
VI. Intercropping	362
VII. Choice of Hybrids.....	364
VIII. Cultivation	365
IX. Irrigation	367

	<i>Page</i>
X. Harvest	369
XI. Farm Drying and Storage.....	372
References.....	375
IX. Production of Hybrid Corn Seed	
JOHN M. AIRY	
I. Seed Corn Producers and Production Practices.....	379
II. Seed Stock Increase.....	382
III. Planting and Growing Seed Corn.....	382
IV. Detasseling Hybrid Corn Seed Fields.....	387
V. Seed Corn Harvest—Field and Plant Operations.....	393
VI. Shelling, Sizing, and Cleaning.....	404
VII. Sales and Distribution Methods.....	417
References.....	418
X. Popcorn	
ARTHUR M. BRUNSON	
I. Origin	423
II. Varieties	424
III. Popping Expansion.....	425
IV. Inheritance of Popping Expansion.....	431
V. Popcorn Hybrids.....	433
VI. Cross Sterility.....	435
VII. Pop-Dent Recoveries.....	436
VIII. Production and Utilization.....	437
References.....	439
XI. Sweet Corn	
GLENN M. SMITH	
I. Introduction	441
II. History	441
III. Uses of Sweet Corn.....	443
IV. Culture	445
V. Problems in Sweet Corn Breeding.....	450
VI. Production of Sweet Corn Seed.....	458
VII. Present-Day Hybrids.....	460
References.....	461
XII. Diseases of Corn	
ARNOLD J. ULLSTRUP	
I. Introduction	465
II. Seed and Seedling Diseases.....	469
III. Stalk and Root Rots.....	473
IV. Ear Rots.....	482
V. Leaf Diseases.....	492
VI. Corn Smuts.....	515
VII. Miscellaneous Diseases.....	520
References.....	527
XIII. The Most Important Corn Insects	
F. F. DICKE	
I. Introduction	537

	<i>Page</i>
II. Research Trend.....	538
III. Soil Insects.....	539
IV. Insects Attacking the Leaf, Stalk, and Ear.....	558
V. Lesser Recognized Groups.....	592
VI. Insects in Relation to Diseases of Corn.....	592
VII. Stored-Grain Insects.....	595
Acknowledgment.....	602
References.....	603
XIV. Industrial Utilization	
G. F. SPRAGUE	
I. Introduction.....	613
II. Wet Milling.....	613
III. Dry Milling.....	627
IV. Fermentation Industries.....	629
References.....	634
XV. The Nutritive Value of Corn	
BURCH H. SCHNEIDER	
I. Introduction.....	637
II. Corn.....	637
III. Differences in Corn.....	638
IV. Chemical Composition.....	638
V. Moisture Content of Corn.....	640
VI. The Protein Content of Corn.....	642
VII. Pellagra and Corn.....	646
VIII. Minerals in Corn.....	647
IX. Vitamins in Corn.....	650
X. Correlations of Corn Nutrients.....	659
XI. The Effect of Disease on Corn's Nutritive Value.....	661
XII. Parts of Corn.....	662
XIII. Grinding Corn.....	664
XIV. Comparison with Other Grains.....	667
XV. The Energy Content of Corn.....	668
XVI. Corn Products Not Discussed.....	669
XVII. Summary and Conclusions.....	670
References.....	670
XVI. The World Production of Corn	
G. F. SPRAGUE	
I. Soil Fertility.....	683
II. Climatic Limitations.....	684
III. Cultural Practices.....	684
IV. Progress in Corn Breeding.....	685
Index.....	689

CHAPTER I

History and Origin of Corn

PAUL WEATHERWAX and L. F. RANDOLPH

I. Early History of Corn and Theories as to Its Origin

Paul Weatherwax

For western civilization the story of corn began in 1492, when, only a few days after the discovery of the island outposts of the New World, Columbus wrote a brief note about this new grain plant and the way in which it was used by the Indians in Cuba. Various accounts of earlier visits to America and earlier European contacts with corn can, for our present purpose, be put aside without prejudice as to their accuracy. Even if they were all true, the fact remains that the events which they recount had no lasting effect on the history of corn.

1. Introduction into Europe

There is still some uncertainty as to when corn first went to Europe. Some historians have made the perfectly plausible statement that Columbus took it to Spain on the return from his first voyage to America, and one painting made many years after the event is said to have included ears of corn among the wonders of the New World which he exhibited at the triumphal reception given for him by Ferdinand and Isabella. A careful search of the old documents, however, has thus far failed to disclose any definite statement on the point in question.

a. Early Published Accounts. It is known that specimens of corn and more detailed accounts of the plant were taken to Spain by members of the second voyage of Columbus, and, as early as 1494, a brief description of it was published in Italy in a little pamphlet of limited circulation. Peter Martyr's account of corn, included in the first of his *Decades of the New World*, in 1511, and again in 1516, effectively brought the plant to the attention of the limited reading public in Europe (Weatherwax, 1945).

During the remainder of the sixteenth century, and extending into the seventeenth, corn appears again and again in the Spanish chronicles of the New World, in the writings of the early settlers in Virginia

and Massachusetts, and in that unique series of European botanical publications known as the *herbals*. The Spanish writers, following the lead of the Caribbean Indians, usually applied to the corn plant the name *maíz*, and from this comes our modern word *maize*. In other European languages the plant appears under a great variety of names, many of which reflect some misunderstanding of it or of its place of origin. Thus we find it called Triticum, Frumentum, Turkish corn, corn of Asia, Welsh corn, Bactrian corn, Indian corn, and many other things.

Apparently the first published picture of the plant was the fine full-page woodcut in Fuchs' herbal of 1542 (Weatherwax, 1951). Some authorities have credited the Spanish chronicler, Oviedo, with an earlier figure, but this claim seems to be without foundation. The figures which appear in one herbal after another for the following two centuries show a great deal of adaptation or outright copying, and the bizarre appearance of some of them shows that the artist often worked from fragmentary or atypical material or let his imagination run wild. A few of them, however, are very good, and, little by little, significant details were accumulated until a composite picture of the species began to emerge.

b. Establishment in the Old World. Meanwhile, the people of the Old World were learning something about the value of corn. At first only a garden curiosity in Europe, it soon began to be recognized as a valuable food crop. Within a few years it spread through northern France, Italy, southeastern Europe, and northern Africa. A locally grown specimen of it was placed in an herbarium in Italy as early as 1532, and another, collected far away along the Euphrates River, bears the date 1574 (Schweinfurth, 1904). The Portuguese introduced the plant along the west coast of Africa early in the sixteenth century and probably took it to eastern India at about the same time. By 1575 or a little later, it was making its way into western China, and, although they recognized it as something new, the Chinese soon began to claim it as one of their native crops. By other routes it had, in the meantime, arrived in the Philippines and the East Indies and was rapidly assuming an important place. In the cool, moist climates of northern Europe and the British Isles it was a poor competitor of the small grains already there or of the potato, which came from America at about the same time.

The upper strata of European populations remained decidedly wary about corn as human food, and the herbalists usually condemn it as the cause of various diseases. As a food for livestock or for the poorer classes of people, however, it soon began to fill a great need. In yield, dependability, and ease of cultivation it was far ahead of most of the food

plants of the Old World in places where it would grow well, and it spread with phenomenal rapidity.

2. *Corn in the Development of Modern America*

On this side of the Atlantic, corn was becoming, in the meantime, one of the main steppingstones to exploration and settlement. The progress of the Spanish conquerors was often measured by the availability of corn to feed their expeditions, and they soon settled down to an economic system in which they made slaves of the Indians and adopted their entire complex of corn cultivation and utilization. Corn bought or stolen from the Indians also served more than once to save the English colonies of Virginia and Massachusetts from starvation. Unlike the Spanish, these English colonists tended to push the Indian aside, to ignore his knowledge of agriculture, and to try to grow corn in their own way, as they had grown the small cereals of Europe. After enduring for a season the ridicule of their clumsy methods by the Indian squaws and the humiliation of having to chop wood and carry water for the Indians in exchange for corn, they learned that they had a new kind of agricultural problem on their hands, laid aside their pride, and took a few humble lessons from the natives.

Following the great herbal period, which coincided largely with the era of discovery and exploration in America, botanical interest in corn subsided for a time. It was given new life toward the end of the eighteenth century by the discovery of the closely related genera, *Tripsacum* and *Euchlaena*. These plants now began to give new point to any consideration of the botanical position of corn and the place of its origin.

a. Development of the West. The principal role of the corn plant during the nineteenth century was in the development of the Middle West. As civilization moved over the Alleghenies with rapidly improving farm implements, the Indians were pacified or driven out, and corn found its rightful home in the woodland clearings and the grasslands of Ohio, Indiana, Illinois, Iowa, and the adjacent states, to a large extent in places where it had not been widely grown in prehistoric times.

b. Pre-Mendelian Corn Breeding. With various mixtures of Indian varieties as a starting point, the farmers of this area, ably led in due time by the agricultural colleges and experiment stations, did a superb job of improving the plant by mass hybridization and selection and adapting the varieties to soils, climates, and specific uses. Much of this work was done more or less blindly, and the mistakes were many; but, on the whole, it got results.

As we now look back at this accomplishment in plant breeding, it has a meaning which was not entirely apparent while the process was

going on. There now emerges a pattern which makes sense in terms of what was then but dimly understood. Continued selection toward a sustained objective produced good results, but it worked much better with some varieties than with others. Results were often better if two good varieties were planted together. The plants of the resulting mixture were usually more vigorous, and the new population was more variable and more amenable to the selective process. We probably oversimplify the story, but there is much truth in it, when we say that the highly successful dent varieties of the Corn Belt resulted in this way from blends of flint varieties of the Iroquois area with soft dent varieties which had migrated northeastward from Mexico.

Something of this sort has apparently happened repeatedly in many places. Many of the high-yielding and adaptable varieties of both North and South America show evidences of such mixed origins. The giant varieties which have been reported, some of them with ears more than 2 feet long, may be suspected of having such an origin, and in the Indian pueblos along the Rio Grande in New Mexico the principle is being demonstrated today. The indigenous varieties which the inhabitants of these towns have for centuries preferred for human food are now being supplemented or replaced with midwestern varieties which give better yields, and the resulting mixtures are at present giving rise to some interesting giant forms.

c. Corn and Modern Genetics. By the end of the nineteenth century the groundwork had been laid for a new chapter in the story of corn. The details of meiosis and fertilization in the angiosperm life cycle had been determined, double fertilization was promising an explanation of xenia, and Mendel had discovered the basic principles of heredity. Biology was ready for a serious consideration of genetics, and in this the corn plant was destined to play an important double role. It had already been a vehicle of the rediscovery of Mendel's laws, and it was soon to make other valuable contributions to genetics. It was also soon to have the newly discovered principles of heredity turned to its own improvement in the spectacular development of hybrid corn.

3. *Corn in Pre-Columbian America*

Corn was by far the most important cultivated plant in America in ancient times. There were many other important food plants—beans, squashes, cassava, peanuts, potatoes, and many other species which are less well known—but, in the total effort spent on them and the values derived from them, corn far surpassed all the others together. It was adaptable to a wide range of soils and climates, had a genetic plasticity which had resulted in the production of almost innumerable varieties

suitable for many different uses, and gave an unusually high yield per man-hour of labor spent on it.

a. Distribution. Early explorations showed that the corn-growing area extended from southern North Dakota and both sides of the lower St. Lawrence valley southward on the mainland and through the West Indies to northern Argentina and Chile. In the present area of the United States it extended westward to the middle of Kansas and Nebraska, and an important lobe of the Mexican area extended northward into Arizona, New Mexico, and southern Colorado.

In the terrain outlined there were, of course, great areas in which, for one reason or another, little or no corn grew. It was sparsely distributed in the Amazon jungles and other very wet tropical regions, and it is a little surprising to learn that, in the great expanse of deciduous forest and prairie of the Missouri-Ohio-Mississippi valley, which is today the greatest cornland of the world, corn was not nearly so important as it was in what would now seem to be the far less favorable deserts of Arizona and New Mexico, the dry limestone plains of Yucatan, and the high valleys of the Andes. We can think of many reasons for this. The Indian had no metal tools and no draft animals to cope with the trees of the forest or the sod of the prairie, and in some otherwise favorable places the depredations of the bison or other herbivorous animals held him in check. There may be still other reasons in the nature of the Indian himself.

b. Varieties and Uses. The great variability of the corn plant led to the selection of numerous widely adapted varieties. Giant forms in the moist tropical lowlands had a growing season nearly a year in length, grew 20 feet tall, and had stalks so large and woody that they were used for building houses. Miniature varieties grown by the Mandans in North Dakota or by the Quechuas at high altitudes in the Andes showed great resistance to cold and could mature in places where the frost-free season was scarcely more than two months in length. Some of the deep-rooted Hopi and Navajo varieties of our Southwest were grown successfully in places where there was almost no summer rain until too late to do much good.

The great range in size, color, shape, and hardness of the grain, to which the Indian still clings in spite of his contacts with our modern varieties, is a bit startling to anyone whose mental picture of corn has been shaped by the prosaic uniformity of the ordinary Corn Belt varieties; and practically all of this diversity was present in the plant long before the discovery of America.

All the major endosperm types—flint, flour, dent, sweet, and pop—had been known in one place or another from time immemorial, and

unquestionably. The geometric form of an ear of corn is simulated by many other plant structures, and an observer who does not have a thorough firsthand knowledge of corn could easily be led astray.

d. American Origin. In all this patchwork of fact, theory, and speculation, we have failed to find a single record of the corn plant, in the form of plant fragment, artifact, or written statement, which is known to have existed anywhere in the Old World previous to the date of the discovery of America. On the other hand, we have good evidence to the contrary. As soon as the plant was introduced into Europe in 1494, it spread like wildfire to areas where it could be grown and where it did not meet with too severe competition from other food plants.

Opposed to any idea that the corn plant originated in the Eastern Hemisphere, there are two impressive categories of facts: its nearest relatives are undoubtedly American, and it was widely distributed here and showed evidence of great antiquity.

e. Tracing Origins. In dealing with most of our economic plants it is possible to find some wild species enough like the cultivated form to suggest the origin and to supply a plausible picture of the changes preceding or accompanying domestication. But corn presents some unique difficulties in this respect. It is peculiarly dependent on man for its survival. Its ear, consisting sometimes of as many as 1000 large grains, firmly attached to a woody cob and wrapped in several layers of husks, is remarkably well adapted to agricultural manipulation but almost completely incapacitated for seed dispersal. A glance at a field of young soybeans where corn grew the year before is enough to demonstrate what happens when corn is left to its own devices for scattering its seeds. The wild corn plant either did not have this handicap or had some sort of compensation for it, and it must at the same time have had sufficient value to the Indian to make it worth while for him to cultivate it.

Certain sources which might be expected to contribute toward the solution of the problem of the ancestry of corn can be marked off as having so far yielded little or nothing. The folklore, agricultural practices, and religious rituals of the Indians tell us nothing except that the native races had been in America for a long time and that corn growing was a very old art (Weatherwax, 1954, Chs. 13, 18). Any knowledge that the early, semicivilized Indian farmer may have had about the wild corn plant and the time and place of its first domestication is apparently completely lost so far as any written or spoken record is concerned. There are no known fossil remains, with the possible exception of pollen grains. Several reports of other fossils have been given more or less serious consideration, but some of the objects have been identified as the remains of other plants than corn, one

turned out to be an embarrassingly misleading artifact (Collins, 1919; Brown, 1934), and some have proved to be mineral specimens in no way connected with corn (Weatherwax, 1935, pp. 9, 10). Archeological remains of the plant are abundant but mostly of too recent origin to be of much value. Certain of these which seem to have some bearing on the problem will be discussed later.

The nature and the distribution of the varieties of corn being cultivated by the Indians at the time of the discovery of America or, for that matter, at the present time, may ultimately contribute to the solution of the riddle, but so far no acceptable pattern of dispersal or evolution has emerged from a study of them. It is probable that for many of them the diffusion from a point of origin had long ago reached an equilibrium and that what variety was grown where was more a matter of the Indian's choice than of natural migration.

5. *Relatives of Corn*

For a hundred years or more it has been customary, in classifying the grasses, to place *Zea*, *Tripsacum*, and *Euchlaena* in one tribe, the *Maydeae*, along with four or five other genera which are all native of southeastern Asia and the adjacent islands. This classification was originally made before much was known about evolution and before much attention was paid to natural relationships. Monoecism, the characteristic on which the unity of the *Maydeae* is based, is now known to occur in many other grasses and is not to be regarded as very significant in defining the larger categories of classification. Some of the American members of the adjacent tribe *Andropogoneae* are doubtless much closer to corn than are these oriental members of the *Maydeae*, and, the more we have learned about the latter, the more inclined we are to disregard them in any consideration of the ancestry of corn (Weatherwax, 1926, 1935, 1950).

The secret of the wild plant from which corn came is to be sought, then, in its relationships with *tripsacum* and *teosinte*, with whatever help we can get from the American *Andropogoneae*. It is also inextricably entangled with the origin and development of the Indian races of America. } ~

a. Teosinte as Putative Wild Corn. Apparently no one has ever seriously considered *tripsacum* as wild corn, and there is no reason why we should do so now. It has been particularly easy, however, to think of *teosinte* in this role. Its superficial appearance is so convincing that many have simply brushed aside the technical objections and accepted it as wild corn. Certain anthropologists, for example, ignoring botanical considerations to the contrary, have written of the great accomplish-

ment of the ancient Indians in domesticating wild teosinte and changing it into corn— or, better still, domesticating “three wild grasses” and producing from them the “three principal varieties of corn” (Gann and Thompson, 1931, pp. 9, 10; Thompson, 1932, p. 22). Only the original authors of that fiction know what the three wild grasses were, or, for that matter, what the three main kinds of corn are.

At least two experiments have been reported in which teosinte was changed into corn by a few generations of selective breeding. From such facts as are available, however, it is evident that both experiments started with hybrids of corn and teosinte rather than with teosinte itself.

The first question which any protagonist of this theory must answer is: Why would the Indian be interested in cultivating teosinte in the first place? He had no domestic animals for which it might provide forage, and its seeds, difficult to harvest and each securely enclosed in a hard shell, were not a promising food material. One mitigating fact about this should, however, not be overlooked. If the fruits of teosinte are heated, they pop in the same manner as pop corn (Beadle, 1939); and, in this process, the shell is thrown off and the edible grain released. If the Indians discovered this trick, it may have given to the plant a food value not generally suspected.

Another way in which teosinte fails to qualify as wild corn is in its highly specialized structure. In having its pistillate spikelets and fruits borne singly, rather than in pairs, on a brittle rachis and in having the grains covered by hard shells and then the spike covered by husks, it has already gone much farther than corn along the road of specialization which the grasses seem to be following. To have changed into something like corn it would have had to do the unlikely thing of undergoing a despecialization in two or three ways, and these changes would have had to occur so closely together that they immediately gave the plant an economic value which it did not previously have.

Teosinte still grows wild and looks so much like corn that we shall always have an uphill task in attempting to convince the lay observer that it is not wild corn. Some future discovery may also compel us to reconsider the whole question, but, at present, those who have seen much of both plants are inclined to look somewhere else for the direct ancestor of corn.

There can be no doubt that teosinte and corn are closely related, even if the one is not the ancestor of the other. The ordinary annual teosinte produces fertile hybrids with practically all varieties of corn. The perennial, tetraploid form crosses with corn, but the hybrids are less fertile. The remarkable thing is that, with this high degree of in-

terfertility, the two genera did not long ago merge into a single complex. We have, however, what we regard as a logical explanation of the mechanism which has kept them separate.

The close relationship between corn and tripsacum is not so obvious externally. In fact, it was not seriously considered until teosinte was found, filling the gap between the two. A morphological comparison of the three genera shows, however, many more similarities than would be expected from external appearances.

b. Hybrid Origin of Corn. Toward the end of the past century, by what now appears as an almost ludicrous mistake, Harshberger (1893) described as wild corn a plant, grown at Harvard University from seeds received from Mexico, which turned out to be a hybrid between corn and teosinte. In correcting his error later (1896) he proposed the alternate theory that corn had originated from a hybrid between teosinte and some unknown wild plant. This idea, that corn was of hybrid origin, was taken up several years later by Collins (1912) and supported by Collins and Kempton in numerous publications. The unknown, hypothetical component of the alleged original hybrid took various forms but was usually pictured as a plant having the general character of pod corn. The vacillating nature of the theory, its failure on final analysis to explain anything, and the fact that no part of it was really necessary caused it to lose support, and it is no longer seriously considered. ✓ Col.

c. Corn-Tripsacum Hybrids. Corn and tripsacum were not known to be interfertile until Mangelsdorf and Reeves (1931) introduced the ingenious technique of shortening the styles of corn and produced a few viable hybrid seeds. Since then, the employment of embryo culture techniques and the use of other species of tripsacum and a wider range of varieties of corn have facilitated the crossing, but the degree of fertility is so low and the procedures are so artificial that the probability of hybridization of corn with any species of tripsacum in nature is remote. The degree of interfertility between tripsacum and teosinte is still lower. Many attempts have been made to cross the two, but only a few have been reported as successful.

A part of the reason for the peculiar position which tripsacum holds in the attempts to make crosses among these three genera may be reflected in its chromosome number. Corn and annual teosinte have 20 as the diploid chromosome number. Perennial teosinte has 40. The lowest number known in tripsacum is 36. One form of *Tripsacum dactyloides* has 36, but the form which crosses most readily with corn has 72. Studies now in progress are showing, however, that its reproductive picture is complicated by a high degree of apomixis and polyembryony,

and in a single colony of the plant, diploid chromosome numbers have been found to range, in multiples of 9, all the way from 36 to 108 (Farquharson, 1954a, 1954b)

d. Pod Corn Probably Not Wild Corn. The successful hybridization of corn and tripsacum, followed by an analysis of the gene difference among corn, tripsacum, and teosinte, laid the foundation for a new theory, which may be summarized as follows (Mangelsdorf and Reeves, 1931, 1935, 1938, 1939): The wild corn plant had essentially the nature of pod corn, and the tunicate character, which has been found in widely separated places in both North and South America, has persisted from ancient times. The Indians domesticated and improved pod corn, and the resulting varieties became widely distributed. At some comparatively recent time, possibly as late as 600 A.D., when the Mayas migrated from Yucatan to the Central American highlands, corn hybridized with tripsacum, giving rise to teosinte. Teosinte then backcrossed with varieties of corn, introducing the latter beneficial germ plasm which had come from tripsacum.

This theory reduces teosinte to the status of a variety of corn which has exchanged a substantial amount of its germ plasm for homologous components from tripsacum. Indeed, in a later publication, the authors of this theory (Reeves and Mangelsdorf, 1942) have proposed that the genus *Euchlaena* be abandoned and its two species be transferred to *Zea*. Fortunately, we believe, this proposal has met with little favor.

Previous to the promulgation of this theory, our thinking about the place of origin of corn had been limited more or less to southern Mexico and Guatemala because it was only there that the ranges of tripsacum and teosinte overlapped. Now, with teosinte removed from the picture, it was possible to broaden the area in which wild corn might have grown. The new theory now points to the eastern slope of the Andes in South America as the most likely place because of an early report of pod corn there (Azara, 1809).

Our principal criticism of this ingenious explanation is that it involves too much theory for the facts. It is top-heavy with premises so interdependent that the failure of any one of them will cause the whole structure to fall. With the facts which we have it would be possible to imagine many different pictures of the origin of the corn plant, but there is something to be said for the simplest picture that will fit all the facts.

The weakest link in the chain of concepts which make up this theory is the position which it gives to pod corn. (See Chapter III.) All the forms of this curious plant which are known today tend to be male sterile when homozygous. They ordinarily reproduce only through

pollination with normal corn. This deficiency has been explained away by assuming that the plant was once normally fertile but that the present male sterility is due to the complex of modern corn characters on which the tunicate condition is superimposed. In testing this point, some progress has been made in bestowing fertility by repeated crossing with certain varieties of corn which are thought to have primitive characteristics. We may pertinently ask whether this procedure may not be interpreted as imparting fertility to a plant which never before had it rather than restoring fertility which had been lost.

It has always been easy to think of pod corn as wild corn. It looks wild. From the trend which evolution is apparently taking in the grass family it will generally be taken for granted that, somewhere in the ancestry of the corn plant, its grains were covered by bracts something like those which cover the grains of pod corn, but that does not necessarily mean that the varieties of pod corn which we have today represent that condition. In the variation of the length of the bracts in a single ear or tassel, in the general effect of the tunicate gene on the growth pattern of the entire plant, and in its male sterility, pod corn seems more properly to belong in the category of anomalies represented by teopod corn and corn grass.

A second weak point in the theory is the improbability that corn and tripsacum would ever have hybridized naturally. All crosses which have thus far been made between the two have involved artificial techniques. The one species of tripsacum which has been crossed with corn does not occur in the area in which teosinte is pictured as originating. The more we have learned about the highly irregular reproductive behavior of tripsacum, involved as it is with polyembryony, apomixis, and chromosomal variations (Farquharson, 1953, 1954a, 1954b), the less likely it seems that it could ever have played the role assigned to it.

The third shortcoming to be mentioned is the question of whether such a cross, between one plant which has 20 chromosomes and an erratic one with 36 or 72, could have given rise to the stable and relatively uniform plant that teosinte is. This remains a question, and a very pertinent one.

Certain corollaries to this theory may also be questioned, although they are not vital parts of it. The great age of the pollen of teosinte reported to have been found in the bog deposits under Mexico City (Barghoorn *et al.*, 1954; Clisby, 1954) and of the fragments of corn showing teosinte contamination which have been found in the caves in New Mexico (Mangelsdorf and Smith, 1949; Arnold and Libby, 1951; Cutler, 1951) calls for a reconsideration of the postulated date of 600 A.D. for the origin of teosinte. To ignore the fact that corn, tripsacum,

and teosinte all occur together only in Mexico and Central America and place the origin of corn several thousand miles away in South America would seem to give undue weight to a pottery artifact of doubtful identity (Mangelsdorf and Reeves, 1939, pp. 246, 247) and a report that pod corn grew there a mere 150 years ago (Azara, 1809). And Cutler's attempt (1944) to make the little hunchback of our southwestern petroglyphs into an Andean flute-playing medicine man who brought pod corn to North America seems too farfetched for any serious consideration.)

6. *Origin of Corn by Divergent Evolution*

Meanwhile, we find nothing wrong with the prosaic, unspectacular idea that corn, tripsacum, and teosinte arose by ordinary divergent evolutions from some common ancestor which possibly gave rise also to some of the *Andropogoneae*. A morphological comparison of the three shows that they are basically alike in structural pattern and that the visible differences among them are due to the differential abortion of organs during development (Weatherwax, 1918, 1935). If we put back the organs which have been lost in evolution, the three converge toward a common type.

Somewhere in the past, along the evolutionary line which led toward tripsacum, something happened to change the basic chromosome number to 9, and this seems to have been followed by the rise of various degrees of polyploidy and many reproductive irregularities. Both basic chromosome numbers, 9 (18) and 10 (20), are also found in the *Andropogoneae*, but so little is known about the members of that tribe that they cannot at present be correlated with the *Maydeae*.

On one of the branches of this family tree, a little nearer to teosinte than to tripsacum, there was a wild plant which was to become the ancestor of corn. Botanists have cherished the hope that the plant was still in existence and might some day be found, but the more we have learned about the whole problem the less likely this seems. When we speculate about the character of this plant, we can do little better than supplement some points in the description of it which De Candolle (1884) wrote three quarters of a century ago.

a. The Hypothetical Wild Ancestor. The wild ancestor of corn was probably a perennial plant with something of the habit of the more caulescent species of *Tripsacum*. Its male and female spikelets were borne in almost completely separated inflorescences, and the lateral, female inflorescences were losing their side branches and tending toward simple spikes. The axes of these spikes had become shortened and thickened, and the pairs of spikelets might already have become ar-

ranged in such a way that they formed an incompletely eight-rowed ear whose cob no longer broke into pieces at maturity. The internodes of the vegetative branch which bore this primitive ear were also undergoing a process of shortening which, phylogenetically speaking, was ultimately to draw the ear down into a covering of husks formed from the leaf sheaths.

The grains of this ear were probably covered by the glumes and lemmas, as they are in most other grasses. It is likely that the abortion of the bracts, leaving the grains bare, was concomitant with the adjustment of the ear to its covering of husks.

If we were to find an ear of such a plant somewhere today, we should doubtless call it pod corn, but it would fall far short of being the monstrosity which we know as pod corn today. It would, on the other hand, be not very different from some of the ears now being recovered from archeological sites in New Mexico. Indeed, among some of the latter, there are ears which seem to show steps in the loss of the bracts.

A plant like this would be of value to the Indian, and we may leave the problem of its domestication and improvement to him. Such a plant would also have most of the biological handicaps which plague the modern corn plant; but, especially if it were a perennial, it might persist for a long time without the help of man.

It is generally conceded that the change from the perennial habit to the annual one is a common course of evolution. In this instance the Indian may have accelerated the process. The most promising plants—those from which seed was most likely to be selected—would be those which quickly came to flower and did not waste time and substance in forming rhizomes or other perennial structures.

b. Place of Origin. We should expect to find this plant—not very abundant—in some isolated locality within the present range of teosinte, that is, in the highlands or foothills from central Mexico to Honduras. The deep ravines at the edges of the plateau would fit the requirements exactly. At the same time teosinte, being well adapted to natural survival, was widely distributed over the highlands of the same area.

When primitive man took over the care of the corn plant and began to sort out varieties adapted to various soils, climates, and uses, he gave it an immense advantage and began an extension of its range which ultimately took it far beyond the natural range of teosinte. The disparity between the two was further increased by the introduction of grazing livestock after the discovery of America; and teosinte is now limited to cultivated fields, thickets of thorny shrubs, and other areas protected from grazing animals.

When corn was first brought from its isolated native habitat out into the better farmlands, where teosinte was already abundant, hybrids between the two doubtless soon appeared, as they do today, and both species might have been expected to lose their identities in a mixed race. But hybrids between the two have about the same handicaps as corn for natural survival and enough of the undesirable characteristics of teosinte to cause them to be weeded out of cultivated fields. Some permanent exchange of genes between the two is usually evident in places where both plants occur, but a difference in the time of flowering of the two and these selective influences of man and nature serve to keep the two pretty well separated.

c. Time of Original Domestication. As to the time at which the domestication of corn first began we have had to revise our ideas many times. The world is much older than we once thought, and all time scales, including the date of the first arrival of man in America, have been greatly extended. De Candolle thought that corn was probably first placed under cultivation about 2000 years ago, but it is now evident that this occurred much earlier.

The radiocarbon method is particularly useful for determining dates within the range involved in this problem, and we should soon have a much better picture of this part of the story. Some of the oldest known remains of fragmentary ears and grains of corn, which have come from caves and rock shelters in New Mexico, are thought to be about 4500 years old. The pollen grains found at depths of more than 150 feet under Mexico City and identified as those of corn, tripsacum, and teosinte, are much older. They doubtless belong to a period many centuries earlier than the beginnings of anything that we can designate as agriculture.

II. Cytogenetic Aspects of the Origin and Evolutionary History of Corn

L. F. Randolph

1. Introduction

Studies of the chromosomes of *Zea* and related genera in recent years have made important contributions to the solution of the difficult problem of the origin of corn. The chromosomes are highly stable entities in which structural and genic changes, when they occur, can be detected by standard cytogenetic techniques. Differences and similarities in number, pachytene configuration, and meiotic behavior of the chromosomes are useful in establishing relationships and reconstructing evolutionary sequences. These techniques have proved their worth in establishing the mode of origin of cultivated varieties of wheat,

tobacco, cotton, sugar cane, and various other important horticultural and crop plants. Unfortunately, they have not been applied as effectively in determining the evolutionary relationships of the corn plant.

Various hypotheses have been advanced to account for the origin of corn, and there is at present no unanimity of opinion concerning the relative merits of these hypotheses. Much of the existing disagreement concerning them has been due to a failure to appreciate fully the significance of cytogenetic data on corn and its relatives that have accumulated during the past quarter of a century. When they are examined in the light of the cytogenetic evidence, the highly speculative nature of hypotheses which assume a complex hybrid origin of corn is clearly apparent. There is little or no support from cytogenetics or cytotaxonomy for the assumptions that it is (1) a hybrid of teosinte and some unknown member of the *Andropogoneae* (Collins, 1912; Harshberger, 1893); (2) an amphidiploid hybrid of Asiatic species belonging to the *Maydeae* and *Andropogoneae* (Anderson, 1945); (3) a trigeneric hybrid of pod corn, *Euchlaena*, and *Tripsacum* (Brieger, 1944); or (4) a recent product of the hybridization of a South American derivative of pod corn and Central American *Tripsacum* with teosinte as a byproduct (Mangelsdorf and Reeves, 1939). On the contrary, the cytogenetic evidence offers no serious obstacles to alternative hypotheses: (1) that *Zea*, *Euchlaena*, and *Tripsacum* originated separately from a common ancestral form (Montgomery, 1906; Weatherwax, 1918, 1935), or (2) that *Zea* was derived from *Euchlaena* by mutation (Ascherson, 1880; Langham, 1940; Longley, 1941b).

There is only the remotest possibility that the progenitor of cultivated corn will ever be found as a relict species in its native habitat. There are relatively few botanically unexplored areas where it could have survived up to the present time. However, it is apparent from the recent discovery of fossil corn pollen in Mexico (Barghoorn *et al.*, 1954) and the earlier discovery of well-preserved cobs and kernels in New Mexico (Mangelsdorf and Reeves, 1945; Mangelsdorf and Smith, 1949) that corn has been indigenous to these regions for many centuries.¹ The identification of additional primitive species of *Tripsacum* in Mexico within the past five years (Hernandez-Xolocotzi and Randolph, 1950; Randolph and Hernandez-Xolocotzi, 1947) places the present center of diversity of the wild relatives of corn in this general

¹ Since this was written a reprint has been received of a recent article by Mangelsdorf (1954) in which discoveries of still more ancient corn remnants were announced. At LaPerra cave in the state of Tamaulipas, Mexico, Richard MacNeish discovered small cobs aged approximately 4450 years, and at Bat Cave, New Mexico, Herbert Dick found smaller and more ancient specimens of corn than were reported previously from the same cave.

area. Certainly, here is the most promising place to look for additional information concerning the early history of corn culture, although it may be too much to expect that a living representative of unimproved, wild corn will be found here or elsewhere.

2. Chromosome Numbers in Corn and Its Wild Relatives

Significant differences in chromosome number are found in the various genera of the tribe *Maydeae* (*Tripsaceae*), to which corn belongs, and in the related tribe *Andropogoneae*, which includes sorghum and sugar cane. Base numbers of 5, 9, and 10 occur in these genera. Polyploidy is prevalent in both the *Maydeae* and *Andropogoneae* (Table I) and has obviously been a significant factor in the

TABLE I
CHROMOSOME NUMBERS IN ZEA AND RELATED GENERA

	<i>n</i>	<i>2n</i>	First authentic count
<i>American Maydeae</i>			
<i>Zea mays</i> L.	10	20	Kuwada (1919)
<i>Euchlaena mexicana</i> Schrad.	10	20	Kuwada (1915)
<i>Euchlaena perennis</i> Hitchc.	20	40	Longley (1924)
<i>Tripsacum floridanum</i> Porter ex Vasey	18	36	Longley (1937)
<i>Tripsacum australe</i> Cutler & Ander.	18	36	Graner & Addison (1944)
<i>Tripsacum maizar</i> Hern. & Rand.	18	36	Hernandez & Randolph (1950)
<i>Tripsacum zopilotense</i> Hern. & Rand.	18	36	Hernandez & Randolph (1950)
<i>Tripsacum dactyloides</i> L.	18	36	Reeves & Mangelsdorf (1935)
<i>Tripsacum dactyloides</i> L.	36	72	Reeves & Mangelsdorf (1935)
<i>Tripsacum laxum</i> Nash	36	72	Reeves & Mangelsdorf (1935)
<i>Tripsacum latifolium</i> Nash	36	72	Reeves & Mangelsdorf (1935)
<i>Tripsacum pilosum</i> Scribn. & Mer.	36	72	Reeves & Mangelsdorf (1935)
<i>Oriental Maydeae</i>			
<i>Coix aquatica</i> Roxb.	5	10	Mangelsdorf & Reeves (1939)
<i>Coix lachryma-jobi</i> L.		20	Longley (1924)
<i>Polytoca barbata</i> Stapf.	10	20	Reeves & Mangelsdorf (1935)
<i>Sclerachne punctata</i> Brown		20	Reeves & Mangelsdorf (1935)
<i>Andropogoneae</i>			
<i>Sorghum versicolor</i> Anders.	5	10	Longley (1932)
<i>Sorghum intrans</i> F. Meull. -	5	10	Garber (1947)
<i>Sorghum dimidiatum</i> Stapf	5	10	Janaki-Ammal (1939)
<i>Sorghum vulgare</i> Pers.	10	20	Kuwada (1915)
<i>Sorghum purpureo-sericeum</i> Schw. & Arch.	20	40	Longley (1932)
<i>Sorghum halepense</i> Pers.	20	40	Longley (1932)
<i>Sorghum randolphianum</i> Parodi	20	40	Randolph (unpublished)
<i>Saecharum officinarum</i> L.	40	80	Bremer (1923)
<i>Manisuris cylindrica</i> (Michx.) Kuntze	9	18	Reeves & Mangelsdorf (1935)

delimitation of species and genera within these tribes. In addition, varying numbers of supernumerary B chromosomes distinctive in morphology and rich in heterochromatin are found more or less fre-

quently in corn (Randolph, 1928), teosinte (Longley, 1937), and possibly also in tripsacum (Maguire, 1952). Various additional types of fragments have been seen in corn (Randolph, 1928) and in sorghum (Janaki-Ammal, 1940).

The reduced or gametic chromosome number in *Zea* and *Euchlaena mexicana* is 10. Among Oriental representatives of the *Maydeae* and *Andropogoneae* this same number is found in species of *Polytoca*, *Sclerachne*, *Coix*, and *Sorghum*. One species of *Coix* and three of *Sorghum* are known to have a gametic number of 5, suggesting that this may be the base number not only for these species but also for *Zea* and related genera in which 10 is the lowest gametic number thus far recorded.

There is, however, very little support from either the cytological or genetical evidence for the suggestion of Edgar Anderson (1945) that corn originated in southeastern Asia as an amphidiploid hybrid of "something like a 5-chromosomed *Sorghum* crossed with some 5-chromosomed relative of *Coix* which spread from Asia to the New World in pre-Columbian times." The morphology of the five pairs of chromosomes of *Sorghum intrans* F. Meull. was studied in the pachytene stage by Garber (1947) and the chromosomes were found to be fundamentally unlike those of corn (Longley, 1941b). They are knobless and their centromeres are indistinguishable when examined with the same aceto-carminic technique that ordinarily renders the centromeres and knobs of *Zea* chromosomes clearly visible. The chromosomes of *Zea* differ in length, with the longest approximately twice as long as the shortest member of the set. Three members of the *S. intrans* set of chromosomes are of approximately the same length; the other two are much shorter and of about equal length. Both of the latter are associated with the nucleolus; one near the mid-region, the other from one-third to one-fourth of the distance from the end of the chromosome. In maize only one chromosome, chromosome 6, which is of medium length, is associated subterminally with the nucleolus.

The only noteworthy similarity in the karyotypes of *Zea* and *S. intrans* is that both have pachytene chromosomes which are favorable for cytological study. But this is not necessarily an indication of close relationship, since other members of the grass family more distantly related to *Zea*, notably rye, have equally favorable pachytene chromosomes (Lima-de-Faria, 1949, 1952).

Another species of *Sorghum* with 10 chromosomes introduced into the United States from Colombia and examined cytologically by Longley (1937) has knobless chromosomes with submedian centromeres and length difference similar to those of corn; the longest chromosome has

a nucleolar organizer near the centromere which occupies a median position in the chromosome. The chromosomes of this species of *Sorghum* are morphologically more similar to those of corn than are the chromosomes of the *S. intrans*.

An additional difficulty for Anderson's suggestion of a southeast Asian origin of corn is that none of the species of *Sorghum* known to have a reduced number of 5 chromosomes is indigenous to that region. *S. intrans* is an Australian species, and the other two are African.

If corn is an amphidiploid, duplicate genes would be expected to be prevalent among the hundreds of mutant loci that have been studied genetically (Emerson *et al.*, 1935). Actually, only 14 cases of duplicate genes, 2 of triplicate, and 1 of quadruplicate genes were listed by Emerson and his co-workers. In a recent analysis of these data Rhoades (1951) found that linkages have been established for both genes of a duplicate set in only 3 of these cases and for each of them both members of the set are in the same chromosome, namely, chromosome 9, which has been suspected of including redundant chromatin (Anderson, 1938; Rhoades, 1945). Recently, Sûto (1952) described the inheritance of a blotched leaf character involving five or more genes, two of which were located in chromosome 6 and one in chromosome 9. Duplicate genes produce 15:1 ratios, but such ratios cannot always be interpreted as evidence of duplicate genes, according to Sprague (1932).

Difficulties involved in the genetic analysis of duplicate and polymeric genes have limited information concerning them. But the available data furnish meager support for the assumption of an amphidiploid origin of maize. In fact, it appears that intrachromosomal rather than interchromosomal duplication has been responsible for most of the duplicate genes in maize, at least for those for which linkage data are presently available.

Another category of genetic effects which apparently involve intrachromosomal duplications of limited extent, but not duplications attributable to amphidiploidy, include the semiallelic (Muller, 1939) or para-allelic (Laughnan, 1952a) genes that are often associated with series of multiple alleles in various organisms. In maize a mosaic pericarp pattern and certain components of the *A* locus are interpreted as sequential duplications of this sort (Laughnan, 1949, 1952b; Sûto, 1952). Similar phenomena in *Drosophila* have been related to the occurrence of repeat bands visible in the salivary chromosomes (Bridges, 1938; Lewis, 1945). These mutants often are inherited as Mendelian dominants. When pronounced position effects are associated with such duplications of limited extent, the result may be a freak or monstrosity, as in the classical case of the bar eye in *Drosophila*.

These examples of duplication associated with dominant phenotypic effects are mentioned here to call attention to the fact that in many respects they are similar to various well-known dominants in maize such as tunicate, teopod, corn grass, sorghum tassel, and tassel seed, to some of which evolutionary significance has been attached by various workers (Mangelsdorf and Reeves, 1939; Singleton, 1951). If these characters originated as simple, Mendelian dominant mutations, they cannot be considered as essential constituents of the residual genotype of the corn plant or as fundamental characteristics of the prototype of cultivated corn (Lindstrom, 1925). The same is true if they are position-effect duplications, as suggested by their appearance, genetic variability, and tendency to sterility when homozygous.

To check the possibility that characters such as tunicate, teopod and corn grass are the expression of duplications in sequence, the sporocytes of plants heterozygous for these genes were examined cytologically at the pachytene stage for loop configurations indicative of duplications. None was seen. This may mean either that duplications were present but too short to produce visible disturbances of synapsis, or that they were not present. Additional studies are needed to determine the genetic nature of such characters and their significance in evolution.

In addition to base numbers of 5 and 10 in the *Maydeae* and *Andropogoneae* a base number of 9 occurs in *Manisuris* and 18 in *Tripsacum*. Since these genera are very similar morphologically, except that *Manisuris* has perfect flowers and those of *Tripsacum* are unisexual, species of *Tripsacum* with $n = 18$ probably should be considered as natural tetraploids, and both *Tripsacum* and *Manisuris* should be placed in the same tribe, as Weatherwax (1935) and others have suggested.

These two genera are the only examples of a deviation from the basic chromosome number of 5 or 10 in either of the tribes to which they belong. It is not known how this transformation was accomplished. The simplest known mechanism is unequal reciprocal translocation whereby long segments of chromatin are transferred consecutively from one chromosome to other members of the set, while at the same time the chromosome in question receives a short segment containing little or no essential chromatin in exchange. After diminution of the chromosome by successive unequal interchanges of this sort reaches the stage when it no longer includes genes required for the survival of the species, the chromosome may be lost without serious deleterious effects. Partial sterility would be expected to accompany such structural changes until they become established in the homozygous condition.

Partial sterility would have far less serious consequences in a perennial, wild species than it would in a short-lived, annual, cultivated plant such as corn, dependent on a high level of productivity for its continued existence.

3. *Allopolyploidy and Autopolyploidy in Tripsacum and Euchlaena and the Relation of Autopolyploidy to the Perennial Growth Habit*

Cytological evidence which has been obtained from pachytene chromosome analyses favors the view that the 36-chromosome form of *T. dactyloides* from Kansas is an allotetraploid. Contrary to the preliminary observations of Longley (1937), pachytene preparations made for me by Jyotirmay Mitra have shown that this species definitely has two satellite chromosomes; one of them is a relatively short acrocentric chromosome with a terminal knob on the long arm, and the other is a much longer metacentric chromosome with a terminal knob on each arm. The nucleolar organizer is near the centromere on each of these chromosomes and is not subterminal as it is on the satellite chromosome of *Zea*. In *T. floridanum* only one chromosome has a nucleolar organizer according to Longley (1937) and is of the acrocentric type found in *T. dactyloides*. Among the 10 pairs of chromosomes in *Zea* and *Euchlaena mexicana* there is but one satellite chromosome pair. In the tetraploid *E. perennis* and in experimentally induced autotetraploid *Zea* there are two satellite chromosome pairs.

The knob number in the Kansas strain of *T. dactyloides* ranges from 22 to 26, and most of the knobs occupy terminal locations on the chromosome, as reported by Longley (1937) for *T. floridanum*. However, in our pachytene preparations of the Kansas strain a terminal pair of tandem knobs previously unreported in any of the *Maydeae* is present; there is also an elongate subterminal knob and beyond it a short, terminal euchromatic segment very similar in appearance to the terminal portion of the abnormal chromosome 10 in maize at it appears in the photograph published by Rhoades (1952).

The regular bivalent synapsis of the chromosomes, the absence of multivalents, and the dissimilarity of the satellite chromosomes in the 36-chromosome form of *T. dactyloides* suggest that this species originated as an amphidiploid of 18-chromosome species now extinct or restricted to some botanically unexplored region of Latin America or the southern United States. Unfortunately, the morphology of 18-chromosome species of *Manisuris*, a close relative of *Tripsacum* from the southern United States and Mexico, has not been investigated.

Since the chromosomes of the 36-chromosome race of *T. dactyloides* from Kansas have terminal knobs on either one or both arms of most

if not all of the 18 chromosomes comprising the gametic complement, it is obvious that if this species originated as an amphiploid both of the parental species must have possessed numerous terminal knobs. The only other known 36-chromosome species with many terminal knobs are *T. floridanum* and *T. zopilotense*. Other 36-chromosome species, *T. australe* and *T. maizar*, are essentially knobless. Both *T. floridanum* and *T. zopilotense* are presently known only from restricted areas, the former in Florida and the latter from Cañada del Zopilote in southwestern Mexico (Hernandez-Xolocotzi and Randolph, 1950). They appear to be relict species formerly with a much wider range of distribution that might have provided an opportunity for them to hybridize.

If the 36-chromosome species of *Tripsacum* are natural tetraploids it follows that the 72-chromosome race of *T. dactyloides* of the southeastern United States and the various 72-chromosome species of *Tripsacum* from Latin America are octoploids. Multivalent synapsis is prevalent among the chromosomes of these species, and much additional evidence of meiotic and other irregularities commonly associated with high levels of polyploidy has been obtained by Farquharson (1953, 1954a, 1954b) from the doubled chromosome form of *T. dactyloides* growing in southern Indiana. Apomixis of the pseudogamous type, polyembryony, and twinning were found to be responsible for the presence in individual colonies of plants with chromosome numbers of 36, 54, 72, and 108. The frequency of polyembryony was as high as 50 per cent in collections of seed from Indiana and Florida, and lower frequencies were noted in approximately 60 collections from widely separated areas extending southward from Indiana and Illinois to Texas, Mississippi, Alabama, Tennessee, Arkansas, Georgia, and Florida.

As a group, the 72-chromosome tripsacums are larger and more vigorous than the 36-chromosome species, and in spite of the observed irregularities in seed production have spread aggressively beyond the present limits of distribution of the parental forms in the United States and also in Latin America. They are probably of too recent origin and too highly cross-incompatible with corn to have exerted any significant influence in recent times on evolutionary trends in cultivated races of corn. Natural hybrids of *Tripsacum* and *Zea* have never been discovered, and special techniques, which include the placement of the *Tripsacum* pollen near the base of the corn silks and embryo culture of the immature embryo, are required to obtain experimental hybrids (Mangelsdorf and Reeves, 1939; Randolph, 1950). Such hybrids when obtained are highly infertile; they rarely produce any functional pollen and only occasional seeds are formed when the hybrid is used as the

female parent in backcrosses to either parent. Further consideration of the evolutionary significance of *Zea-Tripsacum* hybrids will be deferred to a later section.

There is abundant cytotaxonomic and phytogeographical evidence that the 72-chromosome species of Mexican and Guatemalan *Tripsacum* are amphiploids of *T. maizar* and *T. zopilotense* or similar species which have 36 chromosomes (Hernandez-Xolocotzi and Randolph, 1950; Randolph and Hernandez-Xolocotzi, 1947). *T. maizar* is a tall, robust, broad-leafed form with pilose leaf sheaths and very numerous, drooping tassel branches. This species prefers a habitat with sufficient moisture to support a lush tropical vegetation and is known from the region of Acahuižotla, in the state of Guerrero, Mexico. The type localities are 334.5 kilometers south of Mexico City along the main highway to Acapulco and near Arcelia, Guerrero. *T. zopilotense* is a short, grassy, very narrow-leafed species with not more than two or three and often only one terminal spike. This species grows in tufts on the steep, rocky, arid slopes of Cañada del Zopilote, Guerrero, approximately 35 miles from the Acahuižotla station for *T. maizar* in a northerly direction along the main Mexico-Acapulco highway. This is the only locality in which it is known to occur.

Hybrids were obtained from *T. maizar* and *T. zopilotensis* by transferring pollen from plants of *T. zopilotensis* growing at the Zopilote locality to exposed silks of *T. maizar* plants high on the steep slope of the canyon approaching Acahuižotla from the north. Self-contamination was not a problem, as the latter species is protogynous. Seedlings which are now growing at Ithaca, New York, are vegetatively intermediate between the parent species. Under greenhouse culture during the winter months and field culture during the summer they have failed to flower over a four-year period but are vigorous and respond readily to vegetative propagation.

In the general region in which *T. maizar* and *T. zopilotense* occur and extending southward into central Guatemala, eastward to the neighborhood of Vera Cruz, west to Guadalajara, and northward to Tepic, there are numerous local populations of *Tripsacum* with 72 or approximately 72 chromosomes mostly of small numbers of individuals, exhibiting innumerable hybrid combinations of the characters of *T. maizar* and *T. zopilotensis* (Randolph and Hernandez-Xolocotzi, 1950). In collecting herbarium specimens and sporocyte samples for chromosome studies from many of these populations together with Professor E. Hernandez-Xolocotzi, we encountered most frequently colonies that were in general of an intermediate character. Others that exhibited some but not all of the characters of one or the other parent were en-

countered rather frequently. Segregation within populations for such characters as height and amount of branching, amount and kind of pubescence, number of tassel branches and leaf width was frequently noted. An extremely variable population of this sort containing several hundred individuals was discovered along the Guadalajara-Tepic railway from 1 to 2 kilometers north of Tequila.

From extensive field observations supplemented by chromosome counts the conclusion seems obvious that the extreme range in variability noted within and between geographically isolated populations of the 72-chromosome forms was due to the hybridization of 36-chromosome species identical with or very similar to *T. maizar* and *T. zopilotense*, followed by chromosome doubling and subsequent segregation and recombination of characters distinguishing these species (Randolph and Hernandez-Xolocotzi, 1950). This must have occurred long enough ago for the derived allopolyploids to have become widely dispersed, but not long enough ago for them to have become stabilized as taxonomic entities.

The amount and kind of segregation noted in the 72-chromosome populations are most plausibly explained on the assumption that the parent species differed in respect to the characters that are segregating and that their chromosomes were sufficiently homologous to permit partial or complete allosynapsis to occur. Mutation and heterozygosity of the parent species might account for limited amounts of segregation in such populations but certainly not for the very extensive amount observed in many regions throughout the known range of distribution of the 72-chromosome forms.

Multivalent synapsis of the chromosomes in the segregating populations would be expected if the chromosomes of both parents were capable of pairing together as well as *inter se* and thus permit Mendelian segregation of characters by which they differed. Cytological examination of microsporocytes at diakinesis and first metaphase confirmed expectations; varying numbers of quadrivalents and trivalents, usually ranging from 3 to 7, were noted in samples from representative populations.

It is believed that polyploidy with persisting segregation and recombination of morphological and other differences distinguishing the parent species, is the basic cause of the difficulty taxonomists have experienced in defining species of Mexican and Guatemalan *Tripsacum*. This interpretation clarifies the statement of Hitchcock (1922) that *T. pilosum* Scrib. and Merr., *T. lanceolatum* Rupr. ex Fourn., and *T. lemmoni* Vasey form a rather closely connected series, and the more recent comment of Cutler and Anderson (1941) that anything like a final judgment on the entities which make up the genus *Tripsacum*

must await the collection and integration of evidence from several fields. Additional cytotaxonomic studies of these *Tripsacum* populations are needed to determine the validity of these polyploid species.

All of the known species of *Tripsacum* are perennials with a dense, compact rhizome system. Of the two species of teosinte which are recognized, *E. mexicana* is an annual and *E. perennis* is a perennial with elongate, spreading rhizomes (Hitchcock, 1922). The latter species has been reported from only one locality, near Ciudad Guzman in the state of Jalisco, Mexico. Apparently it has disappeared from the type locality, as no specimens could be found there by the writer in 1947. However, plants grown from seed and rhizomes collected by Collins and Kempton at Guzman in 1921 and sent to Professor R. A. Emerson at Cornell soon thereafter are still being maintained by vegetative propagation at Ithaca, New York, and have furnished material for various cytogenetic studies.

This perennial species of teosinte is an autopolyploid with approximately the same frequency of quadrivalent pairing (7 to 9) as in experimentally induced autotetraploid maize. It has two satellite chromosomes of identical form and in contrast to most forms of annual teosinte from Mexico has no conspicuous knobs, either terminal or intercalary. However, plants of Durango teosinte from a stock that has been maintained at Cornell for many years also have been found occasionally without knobs.

It was from such a stock of the annual Durango teosinte grown from X-ray exposed seed that a mutant perennial tetraploid sector developed. This sector included two aerial shoots and a branching rhizome which were organically connected to the base of an otherwise typical annual plant. From this mutant sector a stock was established by vegetative propagation which differed in various plant characters from the original clone of perennial teosinte. It had a more compact, less vigorous, and somewhat dwarfed growth habit. It produced quadrivalents with essentially the same frequency as *E. perennis* and had knobless chromosomes.

Attempts to produce other similar perennial tetraploid sectors from Durango teosinte by additional X-ray treatments of seed were not successful. Tetraploid plants of the same stock of Durango teosinte and also of Florida teosinte, induced experimentally by heat treatments (Randolph, 1932), were typical annuals. Tetraploid corn is also a typical annual, and not perennial, as has been reported erroneously.

Over a period of several years attempts were made to obtain parthenogenetic diploids from *E. perennis* with the use of corn pollen carrying both dominant (*A B Pl Y*) and recessive (*R^g lg*) genes to facilitate the identification of parthenogenetic individuals from both female and

male gametes. From F_1 progenies including approximately 7000 seedlings, two parthenogenetic diploids and one parthenogenetic monoploid were identified. The exceptional diploids were both annuals of a profusely tillering type and did not develop the typical elongate rhizome habit of *E. perennis*; both had 20 chromosomes, exhibited none of the dominant genes of the corn plant used in making the crosses, and were therefore definitely maternal in origin. Unfortunately, neither plant flowered, and both died within a year after vegetative maturity was reached. The parthenogenetic monoploid corn plant developed from a typical teosinte seed. It had the purple plant color, liguleless leaves, and 10 gametic chromosomes of the pollen parent. It developed into a typical, miniature monoploid, similar in growth habit to corn monoploids that have been obtained repeatedly by female parthenogenesis.

Additional evidence concerning the genetic basis of the perennial habit in corn and teosinte was obtained from F_2 progenies of *E. perennis* crossed with experimentally induced autotetraploid corn and with experimentally induced autotetraploid Durango teosinte. The F_1 plants from both crosses were intermediate with respect to growth habit, and the F_2 progenies from both crosses produced mostly intermediates with respect to the perennial habit. In the relatively small populations of a few hundred individuals which were grown, none of the parental types was recovered, indicating that several genes probably were responsible for the difference in growth habit.

No very definite conclusions can be drawn from these experiments and observations on the genetics of the perennial habit in corn and teosinte. The occurrence of the original mutant, perennial, tetraploid sector produced by the annual teosinte plant and the annual habit of the two parthenogenetic diploids obtained from *E. perennis* indicate that tetraploidy and the perennial habit are causally related. The annual habit of experimentally induced autotetraploid Durango teosinte, Florida teosinte, and corn is proof that the perennial habit is not always associated with autotetraploidy in these species. The intermediate habit observed in the F_1 and F_2 progenies of autopolyploid corn and teosinte suggest that several genes are involved in the inheritance of the annual and perennial habit.

In this connection it is noteworthy that Sudan grass, *Sorghum sudanensis* Stapf, is an annual diploid and Johnson grass, *S. halepense* Pers., is a perennial tetraploid. Tetraploids of Sudan grass induced experimentally were typical annuals, and segregating progenies of tetraploid Sudan grass $\times$ Johnson grass were intermediate in character, as in the case of the tetraploid corn and teosinte progenies.

Attempts to utilize the original mutant, perennial tetraploid ob-

tained from Durango teosinte in crossing experiments and to obtain parthenogenetic diploids were not successful, as the plants were lacking in vigor and rarely produced seed under greenhouse culture. Also, F_1 hybrids of autotetraploid corn and the 72-chromosome *Tripsacum dactyloides* included in the experiments were completely male sterile and very highly female sterile and could not be tested for segregation of the perennial habit. As stated elsewhere, hybrids of diploid corn and the 36-chromosome form of *T. dactyloides* are intermediate with respect to the annual and perennial habit, as are plants from backcrosses to corn which possess several tripsacum chromosomes.

4. *Morphological Differences in the Chromosomes of Zea, Euchlaena, and Tripsacum*

Differences and similarities in the form and meiotic behavior of the chromosomes are among the most reliable criteria available for studies of evolutionary relationships. Improvements in cytological techniques and the discovery by Barbara McClintock 25 years ago (1930) that the pachytene chromosomes of corn are suitable for cytogenetic analysis laid the groundwork for the important researches of Longley and others on the morphology of the chromosomes of corn and its relatives.

At the pachytene stage during the mid-prophase of the first meiotic division the chromosomes of the *Maydeae* can be identified by length differences, by arm ratios, and by differences in the size, shape, and position of dark-staining knobs and other less conspicuous structural features. The pachytene chromosomes of corn range in length from approximately 40 to 80 μ as compared to not more than 2.5 to 5 μ for the metaphase root-tip chromosomes. Their centromeres or spindle fiber attachment regions are clearly visible in good pachytene preparations and divide the chromosomes into arms of unequal length.

Since corn can be hybridized with both teosinte and tripsacum, it is possible to make direct comparisons of the morphological characteristics which distinguish their chromosomes. Also, the synaptic behavior of the chromosomes in hybrid combinations furnishes important information concerning chromosome homologies.

The chromosomes of tripsacum are distinctly different from those of corn, with respect to their morphological characteristics that are apparent at the pachytene stage of meiosis. The average length of the tripsacum chromosomes is less than one-half that of the corn chromosomes. Only the four longest chromosomes of *T. floridanum* are as long or longer than the shortest chromosome of corn, and the shortest trip-

sacum chromosome is only about one-third the length of the shortest corn chromosome, according to Longley (1937). There are more chromosomes with subterminal centromeres and fewer with submedian centromeres among the 18 members of the tripsacum set than among the 10 corn chromosomes. In *T. floridanum* Longley noted that the nucleolus is associated with one of the shortest members of the set, with the nucleolar organizer located near the middle of the chromosome; the nucleolar chromosome of corn is of medium length, and has a satellite terminating the short arm, with the organizer occupying a subterminal position on the short arm. The knobs of tripsacum occupy terminal or essentially terminal positions on the chromosomes, whereas those of corn are mostly intercalary. Most of the *Tripsacum* pachytene chromosomes have a more conspicuous concentration of heterochromatin on each side of the centromeres than do the corn chromosomes. It is indeed surprising that tripsacum and corn can be hybridized in view of the many differences which distinguish their chromosomes.

The striking morphological similarity of the chromosomes of teosinte and corn is in marked contrast to the dissimilarities of tripsacum and corn chromosomes. Except for certain differences in knob positions the pachytene chromosomes of corn and teosinte are essentially identical in appearance. Their centromeres occupy the same relative position in each of the chromosomes, and the homologous chromosomes of each set ordinarily are of the same length. The chromosomes of teosinte are not morphologically intermediate between those of corn and tripsacum. They are in fact so similar to those of corn and so dissimilar to those of tripsacum that it seems highly improbable an exchange of segments could have occurred on a sufficiently extensive scale to account for the hybrid origin of teosinte postulated by Mangelsdorf and Reeves (1939).

There have been reports that certain chromosomes of Florida teosinte are slightly longer than those of corn. Kuwada (1919) published figures of F_1 Florida teosinte $\times$ corn hybrids showing heteromorphic bivalents at diakinesis. From similar evidence supplemented by observations on chiasma frequencies in heterozygous translocations involving teosinte and corn chromosomes, Arnason (1936) concluded that there were probably two heteromorphic pairs. Measurements of pachytene chromosome lengths in Guatemalan teosinte from Progreso and Mayuta, which were summarized in the form of diagrams by Longley (1937), showed that in these two varieties chromosome 6 was shorter than in corn. But a direct comparison of the pachytene chromosomes of Florida teosinte with those of corn in an F_1 hybrid revealed only slight length differences, which were most noticeable in chromo-

somes 5 and 9. Later it was stated by Longley (1941b) that from comparisons of the lengths of homologous chromosomes of corn and teosinte, he had concluded that they are not significantly different.

The regular synaptic association of the chromosomes in the particular hybrid of Florida teosinte and corn that was very adequately described by Longley (1937) with accompanying diagrams, drawings, and a photomicrograph of the pachytene chromosomes, furnishes direct cytological proof of the incorrectness of certain basic assumptions made two years later by Mangelsdorf and Reeves (1939) to account for the origin of modern varieties of corn. The assumptions were that many of the most desirable characteristics of these modern corn varieties were acquired through hybridization with tripsacum and that the chromosome knobs of present-day corn also were derived from tripsacum through teosinte (which was assumed to be a corn-tripsacum hybrid) and could therefore be utilized in a precise quantitative determination of the amount of tripsacum contamination.

Obviously, the transfer of knob segments from tripsacum through teosinte to corn would affect the relative lengths of the chromosomes involved in such a transfer and also their synaptic behavior. That such effects have not disturbed the normal paired relationship of the chromosomes and have not produced significant length difference, except possibly in two chromosomes, can be seen by casual inspection of Longley's drawings and photograph of the pachytene chromosomes of the hybrid under discussion. The corn parent of this hybrid contributed to it a set of chromosomes with one or more internal knobs on all but the two shortest members of the set, a total of 10 internal knobs. No terminal knobs were contributed by the corn parent. The set of chromosomes from the teosinte parent had no internal knobs (the enlargement associated with the nucleolar organizer on chromosome 6 is not a typical knob); but there were terminal knobs on one or both arms of all 10 teosinte chromosomes, a total of 12 terminal knobs. Hence, the 20 chromosomes of this hybrid which synapsed to form 10 pairs in meiosis differed with respect to 22 knob-bearing segments.

However, synapsis usually was regular throughout the entire length of the chromosomes and only in two cases were there conspicuous differences in the lengths of the associated homologues. In regions where intercalary knobs were present in the heterozygous condition (where a knob was present on the corn chromosome and none was present on the teosinte chromosome), there is no evidence in Longley's photograph of the loose asymmetrical pairing sometimes seen in corn chromosomes heterozygous for conspicuous knobs.

The regularity of synapsis in this teosinte-corn hybrid, especially

in the regions of the chromosomes which included the internal knobs, appears to invalidate the assumption of Mangelsdorf and Reeves that the internal knobs of modern varieties of corn represent interpolated segments of *tripsacum* germ plasm. If such segments were present, loop configurations characteristic of duplications in the heterozygous condition should have been present, at least in some instances.

Furthermore, there is available no cytological confirmation of Mangelsdorf's contention that corn and teosinte differ chiefly by relatively few chromosome segments or blocks of genes which can be transferred intact, or essentially so except for occasional crossing over, from teosinte to corn by repeated backcrossing of the hybrid to corn. The experiments of Mangelsdorf supporting this assumption are difficult to comprehend, as in one instance it is stated that various amounts of teosinte germ plasm were retained by selection during the backcrossing procedure (Mangelsdorf, 1947, p. 188); elsewhere (p. 187) it is stated that there are no functional aberrations and very little discernible effect in the heterozygous condition. It is not clear how selection could have been practiced under these circumstances. Furthermore, structural chromosomal heterozygosity of the sort postulated by Mangelsdorf might be expected to produce partial sterility, which would be expressed as poorly filled ears, and should also produce loop configurations visible in cytological preparations of the pachytene chromosomes, at least in segments of sufficient extent to permit crossing over. But the heterozygous ears pictured by Mangelsdorf are very well filled. It is unfortunate that chromosome synapsis has not been studied in these hybrids. Since only one parent inbred line apparently was involved in these experiments, and it may have contributed genes responsible at least in part for the partial sterility recovered in the progeny, more information is needed before the significance of these interesting experiments can be evaluated adequately.

In addition to the cytological evidence indicating that the chromosomes of teosinte and corn are morphologically identical, or essentially so, there is abundant genetical proof that the chromosomes of corn and teosinte are very similar in genic composition, regardless of the presence or absence of knobs.

Linkage studies involving teosinte-corn hybrids have included loci of mutant genes widely distributed among the various chromosomes. It is apparent from these studies that the same relative positions in the linkage groups are occupied by the genes of corn and teosinte. The amount of crossing over is essentially the same in the hybrids as in the corn parent. Emerson and Beadle (1932) reported that with the exception of the *C-wx* region of chromosome 9 crossing over occurred in

hybrids of corn and both Florida and Durango teosinte with essentially the same frequency as in corn; in the *C-wx* region it occurred rarely or not at all. In hybrids of corn and Chalco teosinte, crossing over was more frequent in this same region.

Subsequently, Beadle extended the analysis of linkage relations to include both arms of chromosome 9, and found approximately the normal frequency for the long arm (Beadle, 1932). Pairing, chiasma frequency, and crossing over in various chromosome arms of corn $\times$ Florida teosinte hybrids were studied by Arnason (1936) with the aid of a series of translocation heterozygotes. There was approximately 5 per cent of crossing over in the *yg₂-sh-wx* region of the short arm of chromosome 9 which normally occupies 52 map units.

Altogether, tests of linkage relations in corn-teosinte hybrids have included linked genes in 7 of the 10 chromosomes. Normal frequencies of crossing over were reported, with the exception of the short arm of chromosome 9, in which crossing over was markedly reduced. Such reductions in crossover frequencies often are caused by inversions, but in this instance the cause was not determined. Subsequent cytological studies by O'Mara (1942) showed that an inversion in the short arm of Florida teosinte chromosome 9 probably was responsible for the observed reduction in crossing over.

The tests of linkage relations in the corn-teosinte hybrids did not include cytological analyses of knob number or distribution in the stocks used for the tests. But it can be assumed from the numerous surveys that have been made in both corn and teosinte that there must have been a very considerable amount of heterozygosity for knob loci among the hybrids involved in the linkage tests, especially in the corn-Florida teosinte hybrids. If structural alterations of the chromosomes, such as inversions, duplications, or reciprocal translocations, had been prevalent in chromosomes contributed to a particular hybrid by one parent and not by the other, there would most certainly have been disturbances of normal linkage relations. Since such disturbances were detected very rarely, it may be concluded that gene changes rather than structural modifications detectable by genetic tests have been chiefly responsible for the differentiation of corn and teosinte chromosomes.

Specific tests that have been made to determine frequencies of spontaneous structural alterations in corn chromosomes have revealed that they occur very rarely, even in plants from widely separated localities. Alterations such as translocations and inversions which are prevalent in other organisms that have been subjected to intensive cytogenetic analysis are mysteriously lacking in corn. In a search for reciprocal translocations Cooper and Brink (1937) examined plants of

68 varieties of corn from Canada, Mexico, Central America, Peru, and Bolivia. Using pollen abortion as a criterion, they found no translocation in 55 samples. Reciprocal translocations ordinarily produce about 50 per cent aborted pollen when heterozygous and are readily detected by pollen examination.

Inversions in the heterozygous condition produce varying amounts of aborted pollen, depending upon the amount of crossing over in the inverted segment. Thus more careful inspection of the pollen is required to identify them. A study of this kind was conducted by Rhoades and Dempsey (1953), who tested 85 strains of Latin American corn. No translocations were found, and the absence of any appreciable amount of aborted pollen in progenies from these strains was interpreted as proof of the absence of inverted segments long enough to cause detectable amounts of pollen abortion.

Apparently chromosomal rearrangements of the sort that would result in length differences or disturbances of synapsis occur rarely in corn, or if they do occur have been eliminated by the common practice among farmers of selecting for seed only perfectly filled ears. In teosinte human selection has not been involved in the perpetuation of the species, but regular synapsis appears to be the rule in the numerous corn-teosinte hybrids which have been examined cytologically. Thus we have very substantial experimental proof of the absence in both corn and teosinte of the types of chromosomal rearrangements required to support the assumption of Mangelsdorf and Reeves (1939) that the knobs of corn were derived from teosinte, and that teosinte differs from corn chiefly by a number of interpolated segments of chromatin that were assumed to have been derived from *tripsacum*.

5. *Chromosome Knob Number and Distribution in Zea, Euchlaena, and Tripsacum*

The deeply staining chromosome knobs which are clearly visible at the pachytene stage in most species of *Maydeae* are stable structural units occupying fixed positions on the chromosomes (Longley, 1939). In corn these positions or loci are mostly intercalary; in *tripsacum* they are exclusively terminal so far as known, whereas in some forms of teosinte they are intercalary and in others terminal (Longley, 1937).

There are 22 knob-forming loci in corn, of which 18 were identified by Longley in 1939 and 4 have been added since (Longley, 1939; Mangelsdorf and Cameron, 1942; Vachhani, 1950). Eighteen of these loci are intercalary and 4 occupy terminal positions. Knobs occur more frequently at certain loci than at others—a fact which explains the

wide range of variation in knob number in different kinds of corn (Brown, 1949; Longley, 1938; Mangelsdorf and Cameron, 1942).

It was primarily on the basis of chromosome knob relationships that Mangelsdorf and Reeves developed their tripartite theory of the origin of corn (Mangelsdorf and Reeves, 1939; Reeves, 1944). The limited data available at that time indicated that teosinte was intermediate between corn and *tripsacum* with respect to knob number. Longley (1941a) had shown that terminal knobs were present on one or both arms of each of the 18 chromosome pairs of *Tripsacum floridanum* Porter and *T. dactyloides* (L) L., that terminal knobs occurred on 9 of the 10 bivalent chromosomes of Guatemalan teosinte, and that Mexican teosinte had mostly intercalary knobs at loci corresponding to those previously identified in corn. However, we now know that species of *Tripsacum* devoid of chromosome knobs occur in both South America and Mexico (Graner and Addison, 1944; Randolph and Hernandez-Xolocotzi, 1947).

The theory of Mangelsdorf and Reeves (1939) included three basic assumptions: (1) that corn was first developed as a crop plant from pod corn in the Andean region of northwestern South America, whence it was introduced into Central America by man; (2) that teosinte came into existence as a recent product of the natural hybridization of *Zea* and *Tripsacum* in Central America; and (3) that new types of corn originating from this cross and exhibiting agronomically desirable "tripsacoid" characteristics comprise most present-day Central American and North American varieties of corn.

This ingenious hypothesis was a significant contribution to the solution of the problem of the origin of corn. During the 15 years since it was announced in a monographic treatment of the subject, it has stimulated research activity, especially with the wild relatives of corn. Studies of pachytene chromosome morphology and knob distribution have been undertaken on a much larger scale than otherwise would have been attempted. Botanists and archeologists began working together exploring caves and ancient village sites, digging into the debris for remnants of cobs and kernels. Existing varieties of corn throughout the world were compared and their origins traced to fill gaps in our knowledge of their evolutionary history.

Much of the new evidence accumulated since the theory of Mangelsdorf and Reeves was proposed may be interpreted as support for assumptions other than their own, and now that it has been definitely established that wild corn was indigenous to Mexico many thousands of years ago (Barghoorn *et al.*, 1954), studies of the evolutionary history and interrelations of corn, teosinte, and *tripsacum* in this general

region assume added significance. However, these facts should not detract from the beneficial effects of their theory, in having stimulated fundamental research on the corn plant.

The first extensive survey of chromosome knob numbers in different varieties of corn was made by Longley (1938), who reported that the varieties grown by the Indians of the southwestern United States have much higher numbers of knobs than do varieties to the north and east. This was followed by a report on knob numbers in the corn of northwestern Guatemala made by Mangelsdorf and Cameron (1942), who showed that at the lower altitudes of 2000 to 2500 feet where both tripsacum and teosinte occur the native corn had relatively high numbers of knobs. At altitudes in the neighborhood of 8000 feet the native corn had few knobs. Later, Reeves (1944) established a correlation between knob number and distance to the north and south from Central America, where it was assumed that corn had acquired its knobs from contamination with tripsacum. But Reeves' conclusions are of questionable value, as no data were given on the altitudes from which the varieties included in his survey were collected.

To these data from South, Central, and North America should be added the extensive survey by Brown (1949) of United States varieties of northern flints, southern dents, and corn belt inbreds. The 171 strains examined by Brown included most of the major types of United States corn. Knob numbers ranged from 0 to 12, with the highest numbers being concentrated in the southern dents, the lowest in the northern flints, and intermediate numbers in the corn belt lines.

The observed relationship between knob number and altitude in northwestern Guatemala was interpreted by Mangelsdorf and Cameron (1942) to mean that the non-tripsacoid, Andean type of corn originally introduced into Central America was poorly adapted to culture at low altitudes and was replaced by the tripsacoid type as soon as it came into existence. But at higher altitudes the original Andean type, which was later found by Reeves to be essentially knobless, persisted to the present day without tripsacum contamination. According to Mangelsdorf and Cameron northwestern Guatemala was an important secondary center of origin, a place where new types of corn came into existence following the natural hybridization of South American corn with tripsacum in this area.

Likewise, Reeves (1944) did not hesitate to consider the low-knob varieties of central Peru and adjoining areas to be uncontaminated with tripsacum and the high-knob varieties of Guatemala to have received their knobs from natural hybridization with tripsacum. The decrease in the number of knobs of corn in other countries was interpreted as

being roughly proportional to the distance from Guatemala, except in the Andean region, where the primordial corn was considered to have become too well adapted to be displaced by the hybrid mixture from the north.

Unfortunately, these interpretations of knob number in relation to geographic distribution of existing varieties of corn and the assumption that the presence of knobs in corn was proof of recent admixture with tripsacum were based on still other assumptions, implied but apparently overlooked or ignored, by the authors of the tripartite theory in their discussions and interpretations of the evidence on which their theory was based. These other assumptions were (1) that knobs were present in the tripsacum of Guatemala and neighboring regions where the supposed hybridization with knobless South American corn occurred; (2) that the tripsacum and corn of this area were sufficiently cross-compatible to hybridize spontaneously in recent times; and (3) that the observed association of tripsacum and corn chromosomes in the experimental tripsacum-corn hybrids produced by Mangelsdorf and Reeves in Texas provided an adequate mechanism for the transfer of knobs from Guatemalan tripsacum to corn. The first of these additional assumptions is relevant to the present discussion; the others are no less essential to the validity of the tripartite theory and will be considered later.

In considering knob number of corn varieties as one of the most useful characteristics for measuring the degree of tripsacum contamination (Mangelsdorf and Cameron, 1942), the only information on the occurrence of knobs in tripsacum available to the authors of the tripartite theory apparently was the brief description published by Longley in 1938. This account was in the nature of a preliminary report which included a diagram showing exclusively terminal knobs on the chromosomes of *Tripsacum floridanum*. It also included the statement that the study had not reached the stage where a general comparison of the morphology of the tripsacum, teosinte, and corn chromosomes could be made.

My own unpublished observations on the chromosomes of *Tripsacum* have confirmed Longley's observation on *T. floridanum* and have been extended to include both the 36- and 72-chromosome forms of *T. dactyloides* indigenous to the United States as well as various species of Mexican *Tripsacum*. There are abundant terminal knobs on the chromosomes of both forms of *T. dactyloides*. The Kansas form in which there are regularly 18 pairs of chromosomes at diakinesis and first metaphase has from 22 to 26 knobs, the exact number being difficult to determine because of stickiness of the knobs and clumping

tendencies of the chromosomes at the mid-pachytene stage. Since neither *T. floridanum* nor *T. dactyloides* has been reported south of the Texas border, these species could not have been involved in the assumed recent hybridization with corn in Guatemala or neighboring areas.

In 1944 Graner and Addison reported that *Tripsacum australe* Cutler and Anderson is devoid of knobs. This species is widely distributed in South America from Venezuela and Brazil westward into Columbia, Ecuador, Peru and northward to Bolivia and Paraguay (Cutler and Anderson, 1941). It resembles *T. dactyloides* in general appearance and in chromosome number ($2n = 36$) and is the only known South American species of *Tripsacum*. The absence of knobs among Andean varieties of corn cannot be interpreted as evidence that admixture with tripsacum has not occurred.

The two species, *T. zopilotense* and *T. maizar*, described by Hernandez-Xolocotzi and Randolph (1950) from southwestern Mexico are the only other 36-chromosome species known to occur south of the Rio Grande. *T. zopilotense* is a grasslike species resembling *T. floridanum* in growth habit and in having many terminal knobs. *T. maizar* is the most cornlike of any known species of *Tripsacum*. It has a stiff, erect culm with a diameter equal to, or exceeding that, of an average corn plant. The leaves are very broad; the terminal inflorescence or tassel has numerous (15 to 50) elongate, drooping spikes, often branched as in corn and with the number of pistillate spikelets at the base of the spikes much reduced in comparison to other species of *Tripsacum*. This species resembles Andean varieties of corn and northeastern United States flints in having few or no knobs.

The known range of *T. maizar* as definitely established by chromosome counts is at present limited to the state of Guerrero in southwestern Mexico. However, it may extend southward into Guatemala, as plants of similar appearance were seen by the writer in the famous San Antonio Huixta region of northwestern Guatemala while he was exploring that region in 1946, the year preceding the discovery of *T. maizar*. Natural crossing of *T. maizar* with knobless corn brought into Guatemala from South America might have produced new kinds of corn, but there is no reason to suppose that knobbed varieties would have been created.

Detailed analyses of knob number in the 72-chromosome forms of tripsacum prevalent in Mexico and Central America have not been made. But a cursory examination was made of pachytene stages in numerous samples of plants conforming more or less closely to the descriptions given for *T. lanceolatum*, *T. pilosum*, and intermediates conforming to no existing species description which were collected in

many widely separated localities in Guatemala and Mexico. It was apparent that there is an appreciable range in knob number among these forms, of the sort that would be expected if they had originated in recent times as amphidiploids of *T. zopilotense* and *T. maizar*, or similar 36-chromosome species.

It is clear from the experimental evidence on cross-incompatibility of Mexican and Guatemalan tripsacum and corn (Randolph, 1950, 1952) and from the available data on the widespread distribution of corn varieties with few to many knobs that the origin of knobbed varieties of corn must have antedated that of the 72-chromosome forms of tripsacum.

The assumption of Mangelsdorf and Reeves that the chromosome knobs of corn were derived from tripsacum and teosinte seems implausible for the additional reason that in tripsacum and most forms of teosinte the knobs occupy terminal positions on the chromosomes, whereas in corn they are mostly intercalary. In attempting to explain this discrepancy it was assumed originally that a succession of reciprocal translocations was involved (Mangelsdorf and Reeves, 1939). But it is apparent from the studies of Cooper and Brink (1937) and of Rhoades and Dempsey (1953) on the spontaneous occurrence of translocations and inversions that the karyotype of corn is highly stable. No evidence of extensive structural alterations of the sort assumed by Mangelsdorf and Reeves was found in a survey of large numbers of races of corn from widely separated geographic areas. Recently, Reeves (1953) has suggested a still more implausible explanation for the shift of chromosome knobs from a terminal to an intercalary position. His suggestion is that an additional piece of knobless chromatin has "simply become attached" to the knob-bearing ends of chromosomes. Since it is a well-known fact that chromosome fusion occurs only between recently broken ends, this suggestion does not merit serious consideration. The example cited by Reeves in support of his suggestion, namely, the presence of an extra piece on the end of chromosome 10 in certain strains of corn (Longley, 1938), is not a case of an additional segment having become attached to the unbroken end of a chromosome. It is a segment that has replaced the terminal one-sixth of the long arm of chromosome 10, as Rhoades (1952) has clearly shown. This is but one more example of the unfamiliarity with corn cytology that has promoted disagreement in the evaluation of cytogenetic evidence relating to the origin of corn.

Since breaks through the region of chromosome knobs are known to heal just as breaks in euchromatic regions do, it is not difficult to visualize types of inversions or translocations that would shift major

portions of terminal knobs to intercalary regions of the chromosome. If, for example, an inversion were to result from a break passing through the distal region of a terminal knob and another break appreciably nearer the centromere in the same chromosome, the major portion of the knob would be transferred to the internal position at the region of the second break. The distal portion of the knob would remain in its original terminal position, possibly as a rather conspicuous chromomere. Or, an unequal interchange between different chromosomes with one break in a chromosome with a terminal knob passing through the distal region of the knob and the other break much further from the knobless end of another chromosome would produce an interchanged chromosome with an intercalary knob.

Such events would not be expected to have happened in the past on a sufficiently extensive scale to establish races of corn with intercalary knobs, if the structural stability that is characteristic of corn chromosomes at the present time (Rhoades and Dempsey, 1953) prevailed in the past. Structural instability of this sort would be expressed as sterility among interracial hybrids, and morphological dissimilarities in chromosomes readily detectable by cytological means would appear with significant frequencies. The only well-documented example of a spontaneous change in chromosome structure of the sort under discussion is the abnormal chromosome 10 mentioned previously. In this case the change apparently was from a knobless chromosome to one with a terminal knob, or the reciprocal if the abnormal condition was the original one.

The present status of the problem concerning differences with respect to the prevalence of terminal and intercalary chromosome knobs in corn, teosinte, and tripsacum forces one to the conclusion that gene mutation rather than hybridization accompanied by structural chromosomal alterations has produced these fundamental differences in chromosome morphology. A similar conclusion involving gradients was reached by Longley (1939) after a careful comparison of chromosome knobs in teosinte and corn.

It appeared from the observations of Mangelsdorf and Cameron (1942) on races of corn from western Guatemala that various characters associated with high numbers of chromosome knobs prevalent in corn at lower altitudes where tripsacum occurred, were derived from tripsacum as they suggested. Characters of agronomic importance which they found to be associated with relatively high numbers of chromosome knobs included cylindrical vs. pyramidal ears, straight vs. uneven rows, and dent kernels as opposed to flinty or floury types. Brown (1949) reported a positive correlation between high knob num-

ber and high row number, denting, absence of husk leaves, many seminal roots, and irregular kernel rows. However, he concluded that more data are needed before one can safely regard chromosome knobs as a reliable indicator of tripsacum germ plasm, especially as the northern flints which are more "tripsacoid" than any other group of United States varieties have the fewest knobs.

From tests of interrelationships between knob number and various morphological and agronomic characters in 20 inbred lines which were made by Vachhani (1950), no significant associations between knob number and 21 characters were found. Additional tests of the effect of a knob on a particular chromosome showed no association between the presence of any one of several knobs and various plant characters for 70 of 72 tests that were made. These results are not necessarily in conflict with the earlier studies of Mangelsdorf and Cameron, since lower knob numbers were involved in Vachhani's test than were found to be effective in the earlier studies. However, it is perhaps too much to expect, as Vachhani (1950) suggests, that the rather low average number of 4.65 knobs entering a particular cross would have regularly associated with them genes having effects sufficient to establish positive correlations with the characters being studied, especially as most of these characters are polygenic.

It should be obvious from the foregoing discussion that chromosome knobs are of uncertain value as evidence that natural hybridization of corn, teosinte, and tripsacum has been a significant factor in the development of modern varieties of corn. This is due to the equivocal nature of the evidence rather than to any question of the usefulness *per se* of chromosome knobs as a criterion of relationship.

Differences in chromosome knob number may be very useful in establishing relationships among cultivated varieties of corn. Longley (1938) has shown that clues to the geographic origin of varieties of Indian corn may be obtained from studies of knob frequency, and Brown (1949) has made very effective use of knob number in a study of the origin of the dent varieties of the corn belt. In a comprehensive survey of 171 representative strains of corn from different parts of the United States Brown found that corn belt inbreds have knob numbers (2 to 8) that were intermediate between those of old southern dents (5 to 12) and northeastern flints with few if any knobs. These results were interpreted as evidence that corn belt corn varieties originated as hybrids of northern flints and southern dents. Support for this conclusion is available from the historical record and from other incidental sources (Anderson and Brown, 1952).

6. Crossability of Corn and Related Species

Crossability is a useful test of natural relationship if employed in conjunction with other criteria such as morphological and physiological differences. It was formerly assumed by most botanists that good species hybridize rarely or not at all. Now there is general acceptance of the fact that many species that are morphologically distinct hybridize freely and may produce fertile progeny. Even bigeneric hybrids are coming to be accepted as not unusual, although in some quarters there is a tendency to incorporate in the same genus the parent species of bigeneric hybrids. In the case of *Zea* and *Euchlaena* the proposed change (Reeves and Mangelsdorf, 1942) is not warranted. These genera are morphologically distinct entities, more so in fact than many other genera of the grass family, and they have remained distinct even though they are sympatric and may be hybridized readily. Other differences that warrant the retention of separate genera for these species were mentioned in an earlier paper (Randolph, 1952).

It is well known that bigeneric *Zea-Euchlaena* and *Zea-Tripsacum* hybrids have been used extensively in studies of chromosome homologies and other genetic relationships in the *Maydeae*. But it is not so well known that *Zea-Saccharum* hybrids have been produced, thus establishing a community of relationship between the *Maydeae* and *Andropogoneae*. A male-sterile variety of sugar cane, *Saccharum officinale* L., with 40 gametic chromosomes was crossed with pollen of Golden Beauty sweet corn by Janaki-Ammal (1941). Two hybrids were obtained, one of which died in an early seedling stage. The other had 52 chromosomes, including two extra B chromosomes from the corn parent. This second hybrid resembled sugar cane in the seedling stage, but later was more intermediate in appearance and was said to resemble *Tripsacum dactyloides* in growth habit. The *Zea-Saccharum* hybrid was propagated vegetatively for a four-year period but did not produce an inflorescence. The successful hybridization of corn and sugar cane on a much more extensive scale was, however, reported very recently from Formosa by Li, Ma, and Shang (1954). Two hundred and fifty hybrid seedlings, of which 112 survived, were obtained from a male-sterile POJ 2725 variety of sugar cane with 107 somatic chromosomes pollinated by a native variety of white floury corn. The hybrids were phenotypically intermediate in most characters and had from 112 to 127 chromosomes, including one set of 10 from corn and somewhat more or less than two sets from the sugar-cane parent.

Interest in problems of hybridity is currently producing a con-

siderable volume of literature concerned with assumed "tripsacoid" characters of corn (Anderson and Erickson, 1941) and with attempts to demonstrate that "introgression" of teosinte into corn, by which is meant simply the transfer of characters from one species to the other, has been the source of many of the desirable characteristics of modern corn varieties. An alternative interpretation is much less involved; namely, that parallel mutation accounts for the occurrence of similar characteristics in corn, teosinte, and tripsacum. Obviously, these species must have many genes in common or they could not be hybridized. The concept of identical mutations occurring at the same loci in these species offers an entirely adequate and much simpler explanation of their phenotypical similarities than does that of the transfer through numerous hybrid generations of specific character from one species to another under natural conditions.

Corn is a notoriously mutable species, segregating for large numbers of mutants when self-pollinated. Field observations of teosinte and tripsacum where both are of widespread occurrence in Mexico and Guatemala over a period of several years have convinced me that they too are segregating for many of the same mutants that have been identified in corn. Also, we have direct proof from the linkage studies of teosinte-corn hybrids (Arnason, 1936; Beadle, 1932; Emerson and Beadle, 1932) that the positions of many different gene loci are the same in corn and teosinte and that the same alleles are present in both species. Therefore, it seems much more plausible to assume that the occurrence of similar characters in the three species under consideration is due to mutation involving identical or similar alleles rather than to a transfer of genes from one species to another.

In connection with this problem there has been too much speculation and too little field study of teosinte, tripsacum, and corn in areas where all three species are sympatric. When such studies are made, much evidence appears in support of the concept of parallel mutation. For example, high-altitude corn of 9000 to 10,000 feet in the neighborhood of Mexico City is red in color owing to the presence of strong dominant alleles at the B locus and to high light intensities which bring the character to full expression. At a much lower altitude just south of Acahuizotla far removed from any sun-red types of corn may be found small colonies of a mutant sun-red tripsacum in the midst of scattered populations of normal green plants. This same high-altitude corn has tassels reduced to but one or two spikes, which is the prevailing tassel-type of the more grasslike tripsacums of lower altitudes. Very few tassel branches also characterized some of the early inbred lines of Cornell 11, Lucas Favorite, and other commercial varieties of flint corn

of the northeastern United States. Mutation and segregation of genic components of the corn plant itself is for me an entirely adequate explanation of the resemblance of these tassels of corn and certain species of *Tripsacum* and is preferable to the nebulous notion that introgression has been involved. The arguments advanced by Anderson and Erickson (1941) that such "tripsacoid" characters cannot be due to mutation because they are mostly recessive in corn and do not occur in the Andean region carry little weight. Most corn mutants are recessives; and the argument that Andean corn is non-tripsacoid because it has no knobs is invalid, since knobless *Tripsacum australe* is widespread in South America (Graner and Addison, 1944).

There is no doubt that corn and teosinte do hybridize rarely in both Mexico and Guatemala, but adequate cytogenetic proof that such fortuitous hybridization has done anything more than produce occasional admixtures of germ plasm in restricted populations of corn and teosinte is conspicuously lacking. Although teosinte is found growing as a weed in corn fields throughout its range of distribution in Guatemala and Mexico, it very definitely retains the essential characteristics of the species throughout its entire range. Genetic barriers to crossability and the lack of any significant amount of gene transfer from one species to the other are preserving its identity as a good species.

It has been demonstrated repeatedly that corn and teosinte can be hybridized readily and that the hybrids are completely fertile or nearly so. Furthermore there is intimate and regular synapsis of most of the chromosomes in the F_1 hybrids of corn and both Mexican and Florida teosinte (Beadle, 1932; Longley, 1937), and with the exception of the short arm of chromosome 9 crossing over occurs with the same frequency in the first-generation hybrids of teosinte and corn as in corn itself (Arnason, 1936; Beadle, 1932; Emerson and Beadle, 1932). But from these experimental data it does not necessarily follow that corn and teosinte are hybridizing freely in nature, even though teosinte almost invariably is found growing in close proximity to corn, often as a weed in corn fields, and both flower at the same time.

In searching for spontaneous teosinte-corn hybrids the neighborhood of the village of Chalco near Mexico City seemed to be the most favorable place to look. Longley (1937) had reported that Chalco teosinte has intercalary knobs as in corn; this was interpreted to mean that they were or had been hybridizing freely. Longley also found that both Florida and Guatemala teosinte have terminal knobs as in *tripsacum*, indicating that they were less or not at all contaminated by corn, since corn has mostly intercalary knobs. Also, Mangelsdorf (1952, p. 184) found three undoubted hybrids at Chalco in 1943.

My first visit to Chalco was in January, 1942, after the corn harvest was completed. Teosinte was abundantly evident as a weed that had been left in fields from which the corn plants had been removed. I could find no teosinte-corn hybrids; all of the plants I saw had the typical clusters of tiny ears with few seeds that shattered freely.

My next visit to the Chalco area was in the late fall of 1947 when the corn was approaching maturity but harvest had not yet begun. Several large fields were inspected in which teosinte was present as a weed and especially abundant at the edges of the fields. Many plants were inspected in search of ears showing evidences of hybridity. Not one first-generation hybrid was found, and other evidences of hybridity were lacking, except for an occasional teosinte plant with yellow endosperm typical of the corn of the region and varying amounts of sun-red plant color or hairiness of leaf sheaths that the corn and teosinte have in common in the vicinity of Chalco.

Teosinte is not only abundant as a weed at Chalco but is also grown for fodder in fields adjoining the corn fields. Such fields of teosinte are a very favorable place to look for spontaneous teosinte-corn hybrids. There could not possibly be any selective elimination of hybrid seed produced by wind-borne corn pollen on pure teosinte plants harvested the previous year for seed, since hybrid seeds would be indistinguishable from nonhybrid seeds. Permission was obtained from a farmer to inspect a field of teosinte in the Chalco area that he had commenced to harvest as green fodder. The plants had produced a dense, rank growth surprisingly uniform in height, leaf width, number of tassel branches, husk number, and other characters. Tiny ears and very small seeds enclosed in the triangular rachis segments typical of Mexican teosinte were uniformly present. There must have been many thousands of plants in this field of pure teosinte, but I could find no hybrids among them. First- and second-generation teosinte-corn hybrids are unmistakable, exhibit hybrid vigor, and would not be overlooked by anyone who has produced them experimentally. My experience at Chalco convinced me they are very rare in this area. However, hybrids were found in Guatemala where others had failed to find them (Kempton and Popenoe, 1937).

The occurrence of thousands of acres of teosinte near San Antonio Huixta in northwestern Guatemala as the dominant plant in the landscape was reported in 1935 by Kempton and Popenoe (1937). Along with the announcement of their discovery these investigators reported that their search for natural teosinte-corn hybrids in this area was unsuccessful.

In November, 1946, I visited this same region with Dr. George

Semeniuk of the Iowa State College-Guatemala Tropical Research Center. We were equipped with provisions, pack animals, and guides for five days of travel and exploration over the mountain trails of this area to study the corn, teosinte, and tripsacum of the region and look for natural hybrids. After a prolonged search 2 F_1 hybrids of teosinte and corn were found within a few feet of each other near the crest of the hill above the village of Najoya. On the opposite slope above the village of San Antonio Huixta a total of 19 F_1 hybrids were identified in fields bordering the trail leading to Jacaltenango. Further along the trail, near the upper limit of teosinte in this locality, an additional group of 24 F_1 plants and 3 F_2 plants were seen. These hybrid plants were from 8 to 12 feet tall and in comparison to nearby plants of pure corn and teosinte exhibited pronounced hybrid vigor.

Conditions were especially favorable for natural hybridization to occur in this area. Small fields of corn in various stages of maturity were scattered over hillsides surrounded by waste land with teosinte the dominant plant outside the cultivated fields. Also, teosinte was growing largely unmolested as a weed in the corn fields, and it was obvious that both species had been flowering simultaneously over a considerable period of time.

Tripsacum was not seen in the Najoya-San Antonio Huixta region. But in the direction of Petatan a form with narrow leaves, possibly *T. lanceolatum* Rupr. ex Fourn., was seen on dry, rocky slopes for a distance of several kilometers beginning near Petatan and extending to within approximately 3 kilometers of San Antonio Huixta. A form with broad leaves and pilose basal leaf sheaths which might have been either *T. pilosum* Scribr. and Merr. or *T. maizar* Hern. and Rand. was also seen in open woodland areas midway between San Antonio Huixta and Petatan, and again near Santa Ana. Identification was uncertain, as these plants were at a stage of maturity too late for sporocyte chromosome counts and too early for other diagnostic characters to be well developed. We did not encounter the species with broad leaves which Kempton and Popenoe (1937) saw growing in this general region and suggested might be *T. laxum* Nash.

Nowhere was tripsacum seen growing in close proximity to either teosinte or corn, and although a careful search was made for them, no plants were found that could possibly have been either *Tripsacum-Zea* or *Tripsacum-Euchlaena* hybrids. In fact, such hybrids have never been reported by any of the various botanists who have explored the areas of Mexico and Guatemala where teosinte and tripsacum occur, in search of evidence on the origin of corn. If teosinte originated from the natural crossing of tripsacum and corn in northwestern Guate-

mala, as postulated by Mangelsdorf and Cameron (1942), they must have occupied similar habitats much more extensively than they do at present, and they must have been more cross-compatible (Randolph, 1950, 1952).

The discovery of an appreciable number of *Euchlaena-Zea* hybrids in the San Antonio Huixta area is especially noteworthy. Longley (1938) found no cytological evidence from knob distribution on teosinte chromosomes that suggested an amount of contamination of teosinte with corn in this area comparable to that found in Mexican teosinte, which has chiefly intercalary knobs as in corn. He examined teosinte from various regions of Guatemala, including San Antonio Huixta, and all had exclusively terminal knobs. Guatemalan teosinte has been considered by most workers to be free of contamination with corn because it has only terminal knobs, and the presence of intercalary knobs has been interpreted as evidence of contamination by corn.

The knobs of corn varieties at San Antonio Huixta must be predominantly intercalary, since Mangelsdorf and Cameron (1942) in a comprehensive survey of knob number in Guatemalan corn noted only a single terminal knob position in addition to the two already known (Longley, 1952). The observed differences in knob distribution of Guatemalan teosinte and corn suggest that there has been little or no significant mixing of germ plasm in either Guatemala or Mexico, even though natural crossing occurs in both countries.

Much emphasis has been placed on the intermediate nature of teosinte by the proponents of the view that it originated as a hybrid of corn and teosinte (Mangelsdorf and Reeves, 1939; Mangelsdorf and Smith, 1949; Reeves, 1953). But with respect to such highly significant and very stable cytological features as number and length of the chromosomes, the teosinte of Mexico and of Guatemala in the region where it is supposed to have originated as a tripsacum-corn hybrid (Mangelsdorf and Cameron, 1942) is not intermediate between the putative parents of the same general region for any one of these characters.

The cytological evidence that is now available and my field observations on the results of natural crossing strongly support the conclusion that there has been much less "introgression" of teosinte into corn than has been generally assumed. Differences with respect to the most conservative structures of these species—their reproductive organs, especially the seed and the ear, and their chromosomes—certainly are of much greater value in determining genetic relationships than are vegetative structures. The more conservative organs are very different in corn and teosinte.

7. *Experimental Hybrids of Corn and Tripsacum dactyloides*

No spontaneous *Zea-Tripsacum* hybrids have been found anywhere throughout the very extensive range of the genus *Tripsacum* from the central United States southward into northern and central South America. But experimental hybrids can be produced with special crossing techniques, which were first developed by Mangelsdorf and Reeves (1939). This was a highly significant accomplishment since it opened the door to a broad new field of cytogenetic research.

We have confirmed the results of Mangelsdorf and Reeves with respect to the crossability of United States varieties of corn and *Tripsacum dactyloides*, a species which is endemic to the United States and has not been reported south of the Mexican border. Their crossing technique was simplified and improved, and several hundred hybrids were produced for cytogenetic study. In making the pollinations it is only necessary to slit the husks of the corn ear shoots longitudinally from the tip downward in two or three places and open the husk segments sufficiently to sift a mixture of tripsacum and corn pollen onto the corn silks near their attachment to the ovary. The husks are then secured in their original position by wrapping them in glassine paper fastened with rubber bands. Corn pollen marked with dominant endosperm and aleurone genes was mixed with the tripsacum pollen to produce a few normally developed corn seeds on the ear to stimulate cob growth. As much as a quarter or more of the pollen mixture can be corn pollen and still not produce more than a few scattered corn seeds on the ear. Apparently, the tripsacum pollen tubes usually reach the embryo sac sooner than those of the corn pollen and prevent most of the latter from functioning. Between two and three weeks after pollination the immature hybrid embryos have reached their maximum development *in situ*. They are then excised and germinated with the embryo culture technique developed originally for iris seed (Randolph, 1945).

We have produced many hybrids of diploid corn and both the 36- and 72-chromosome forms of *T. dactyloides*. We have also produced the amphidiploid hybrid, $4n$ corn $\times$ 72-chromosome *T. dactyloides*. All of these hybrids are completely male sterile and highly female sterile in backcrosses to corn, including the amphidiploid. As reported by Mangelsdorf and Reeves (1939) the hybrid of $2n$ corn $\times$ 36-chromosome tripsacum occasionally produces viable seeds exclusively from unreduced female gametes of the F_1 hybrid in combination with a normally reduced male gamete of the corn plant used for the backcrosses.

The 38-chromosome, first-generation backcross plants are more fertile than the F_1 and when pollinated by corn produce normally reduced

female gametes with a complete set of corn chromosomes plus varying numbers of extra tripsacum chromosomes. From these extra-chromosome plants, individuals have been isolated by successive backcrossing to corn which have 20 corn chromosomes plus one tripsacum chromosome. These extra-chromosome plants have been utilized by Maguire (1952) for studies of synapsis and the cytological demonstration of crossing over between tripsacum and corn chromosomes, and to determine phenotypic effects on corn of extra tripsacum chromosomes.

Another objective in these cytogenetic studies of tripsacum-corn hybrids was to see if it would be possible to recover an annual, true-breeding type at all similar to annual teosinte. This should be possible if the assumption of Mangelsdorf and Reeves (1939) is true that teosinte is a recent product of the hybridization of corn and tripsacum. The F_1 hybrid plants do not even remotely resemble *Euchlaena*. They are semiperennial and can be propagated indefinitely by subdivision of the dense clumps that are produced by the more vigorous hybrid plants. The spikes of the terminal inflorescences are few in number and bear pistillate spikelets at the base of otherwise staminate spikes. The spikelets are paired as in corn. Their general growth habit is very different from that of teosinte, and as stated previously they are completely male sterile.

In the advanced-generation progenies backcrossed to corn the plants resemble corn more and more closely as the tripsacum chromosomes are lost. Nothing approaching a true-breeding, teosinte-like plant has been recovered in any of these stocks. Loss of the extra tripsacum chromosomes leaves no trace of tripsacum germ plasm that can be detected in the phenotypic appearance of the plants.

However, cytological studies of plants carrying extra tripsacum chromosomes have demonstrated that synapsis and crossing over between tripsacum and corn chromosomes does occur at very rare intervals (Maguire, 1952). It was possible to demonstrate crossing over cytologically, since most of the corn chromosomes do not have terminal knobs and those of *T. dactyloides* do have terminal knobs on one or both arms. The case described by Maguire involved a short tripsacum chromosome with a terminal knob on the long arm that synapsed with the knobless short arm of corn chromosome 2. As the result of crossing over the knob-bearing terminal segment of the tripsacum chromosome exchanged places with a knobless terminal segment of chromosome 2 of corn. Plants with 20 chromosomes including a knobbed chromosome 2 were indistinguishable from sibs with the normal complement of corn chromosomes. Furthermore, comparative studies of the phenotype of plants trisomic for seven different tripsacum chromo-

somes and their disomic sibs made by Maguire revealed little or no evidence of any phenotypic effect of these isolated chromosomes derived from *tripsacum*.

These results are not in agreement with those of Mangelsdorf and Reeves (1939), who observed various phenotypic effects of *tripsacum* chromosomes in plants carrying two complete sets of corn chromosomes. This may be due to the fact that different *tripsacum* chromosomes were involved in the two series of tests.

The salient features of the *tripsacum*-corn hybrids most directly related to the evolutionary history of corn may be summarized as follows: (1) Such hybrids can be produced only by utilizing special crossing techniques and by embryo culturing the seed. (2) The hybrids are phenotypically very different from teosinte, and nothing resembling a true-breeding, annual teosinte has been derived from them. (3) The F_1 hybrids are highly sterile, and only unreduced eggs function in backcrosses to corn. (4) None of the extra-chromosome plants produced by successive backcrossing to corn are stable true-breeding types resembling teosinte; the extra chromosomes are transmitted with a low frequency by the seed parent only and disappear rapidly in succeeding backcrosses. (5) Synapsis and crossing over between restricted regions of certain *Zea* and *Tripsacum* chromosomes have been demonstrated cytologically. Crossing over occurs with a very low frequency, indicating that most of the observed association between *Tripsacum* and *Zea* chromosomes at meiosis is fortuitous and does not involve true synapsis followed by the expected frequency of crossing over. In this connection it should be noted that bivalents or trivalents at diakinesis and first metaphase involving *tripsacum* and corn chromosomes are not necessarily proof that crossing over has occurred between them; forces other than chiasmata may be involved, as reported in other organisms.

8. Tests of Crossability of Guatemalan and Mexican *Tripsacum* and Corn

The production of experimental hybrids of corn and *Tripsacum dactyloides* by Mangelsdorf and Reeves (1939) was an outstanding contribution to studies of the evolutionary history of corn. This is a very wide cross, and special techniques were required to obtain the hybrids. This accomplishment led to the development by these authors of the highly speculative hypotheses that (1) modern varieties of Central and North American corn possess agronomically significant admixtures of *Tripsacum* germ plasm, and (2) that *Euchlaena*, the closest relative of maize, is a recent product of the natural hybridization of *Zea* and *Tripsacum* which occurred after cultivated maize had been

introduced by man into Central America (Mangelsdorf and Cameron, 1942, p. 217).

There is no very convincing cytogenetic evidence that the "tripsacoid" characteristics attributed to corn inbreds by Anderson and Erickson (1941) were derived from tripsacum by hybridization. More convincing arguments have been advanced by Mangelsdorf and Reeves in support of their contention that characters of very great economic importance such as resistance to heat, drought, cold, insect pests, and diseases, and others of less importance such as lengthening of the ear and straightening of the rows of grain, were derived from tripsacum. However, their arguments were based on the assumption that tripsacum and corn are cross-compatible in Central America where both *Euchlaena* and *Tripsacum* are indigenous, an assumption that is no longer valid, in view of the negative results that have since been obtained from attempts to make such crosses (Randolph, 1950). The "tripsacoid" characters of modern corn can be explained more simply and plausibly as the products of mutation and selection within corn itself during the many centuries of its existence as a cultivated plant, without resort to an explanation involving intergeneric hybridization and a third genus as an essential intermediary.

With respect to the genetic relationships of tripsacum and corn in Guatemala and Mexico, there is now ample proof that the existing primitive, unimproved races of Indian corn and the tripsacum of the same localities are highly cross-incompatible (Randolph, 1950). Tests of crossability which were made in Guatemala and Mexico from 1946 to 1949 demonstrated the presence of a genetic isolating mechanism that effectively inhibits intercrossing among these species and has undoubtedly been an important factor in the evolution of maize as a separate entity in the midst of its wild relatives.

The 1946 tests involved three local varieties of corn and the native 72-chromosome tripsacum, probably *T. lanceolatum* Rupr. ex Fourn., in the neighborhood of Guatemala City and Antigua. A total of 150 ear shoots and an estimated 29,000 female gametes were involved in these tests which produced no hybrid seed with viable embryos. In 1947 and 1948 primitive or unimproved varieties of native corn at three widely separated localities in central and western Mexico, Puente Grande, Tequila, and Chapingo, were crossed with four distinct types of *Tripsacum* that were growing in these areas. Again, no hybrids were obtained from 167 pollinations, including tests of an estimated 28,000 female gametes. The 1948 trials included an additional extensive series of tests with the two diploid species, *T. maizar* and *T. zopilotense*, but the 80 pollinated ear shoots were almost completely destroyed by insects,

and only portions of ears with less than 1500 functional ovules could be scored, none of which produced viable seed. A final series of tests in 1949 at Progreso, near Cuernavaca, Mexico, gave positive results to the extent that two viable seedlings were obtained by embryo culture from a total of more than 72,000 female corn gametes tested. Approximately 14,500 of these were produced with pollen of *T. maizar*, 15,000 with pollen of *T. zopilotense*, and the remainder with seven distinct types of 72-chromosome tripsacum from central and western Mexico. Five races of corn were used in the tests with *T. maizar*, six with *T. zopilotense*, and nine with the 72-chromosome tripsacum. Most of these corn stocks for the 1949 tests and those for the 1947 tests at Chapingo were very generously made available by E. J. Wellhausen of the Rockefeller Foundation in Mexico. They were selected as being representative of unimproved native races of Mexican corn. In addition, a Celaya synthetic variety developed by the Foundation was included in these tests.

Results of similar crosses of *T. dactyloides* at Ithaca, New York, during this same period indicated that the chance of obtaining hybrids was better with the use of hybrid corn stocks than with inbreds as seed parents. The only two hybrid seedlings obtained from the four-year series of tests in Guatemala and Mexico were from the Celaya synthetic hybrid, and not from the unimproved native races of corn. The same techniques of pollination and embryo culture that had been successful in producing hybrids of *T. dactyloides* and corn at Ithaca, New York, with a frequency ranging from a fraction of one per cent to as high as 25 or 30 per cent were used in making the Mexican and Guatemalan crosses. For positive identification, chromosome counts were made from root tips of any seedlings suspected of being hybrids.

From the negative results of the tests conducted in Mexico and Guatemala it was concluded that primitive corn and tripsacum probably have existed together without significant amounts of natural crossing for long periods of time in Mexico and neighboring regions, and that corn probably originated in this area. With respect to the corn plant at least, Vavilov (1931) was correct in assuming that the primary centers of diversity for cultivated plants are characterized by the absence of interspecific hybridization. It is probably also true, as he assumed, that dominant mutants tend to be concentrated at the primary center of diversity, and recessives at the periphery.

It was also concluded that the crossability tests with corn and tripsacum conducted in Guatemala and Mexico do not support the hypothesis of Mangelsdorf and Reeves with respect to the hybrid origin of teosinte. This conclusion was challenged by the junior author of the tripartite hypothesis with the statement that "Randolph's experiments

are not a critical test of *any* hypothesis, and, in fact are essentially meaningless." Perhaps the lack of appreciation of what constitutes a meaningful test explains the failure of the originators to undertake the experimental verification of the central feature of their tripartite hypothesis during the interval since it was proposed 15 years ago.

The negative results of these tests exclude the possibility that important characteristics of corn belt corn have been derived from the recent admixture of *tripsacum* germ plasm in the Mexican-Guatemalan region, as postulated by Mangelsdorf and Reeves. It is true that two hybrid seedlings were obtained after repeated trials. But these hybrid plants have never bloomed, and it is probable if they had that they would be highly sterile, as indicated by the performance of hybrids of corn and *T. dactyloides* obtained in the United States. Furthermore, to produce the two hybrid seedlings the placement of the pollen at the base of the silks of earshoots from which the husks had been withdrawn was required, and in addition it was necessary to culture the immature embryos on sterile nutrient agar after they had attained their maximum development on the ear. Such favorable conditions for promoting successful hybridization could not occur in nature.

The pronounced difference between the Mexican-Guatemalan *Tripsacum* and *T. dactyloides* of the United States with respect to the degree of cross-compatibility demonstrated by the crossability tests was highly significant for all of the species involved in the tests. The lowest number of gametes tested for any species was approximately 15,000 for both of the 36-chromosome Mexican species, *T. maizar* and *T. zopilotense*, and no hybrids were obtained from either of these species. This is in marked contrast to the relatively high frequency with which hybrids were obtained from both the 36- and 72-chromosome forms of *T. dactyloides*.

The existence of genetic barriers to crossability at the present center of diversity for the American *Maydeae* suggests that they have been an important factor in the divergent evolution of corn and its wild relatives. It is probable that at the center of diversity of the American *Maydeae* in Mexico these cross-incompatibility factors had high selective value in establishing crossability barriers between coexisting species as they evolved from less specialized ancestral forms. Also, it is possible that *Tripsacum* was effectively isolated from *Zea* by ecological, geographic, or other factors at the periphery of its range in the United States, and in the absence of any appreciable selective value cross-incompatibility genes did not become established in this area.

These interrelationships of corn and *tripsacum* with respect to crossability, that have been established by experimentation, add substantial

support to the theory of independent origin of *Zea*, *Tripsacum*, and *Euchlaena* from a common ancestor (Montgomery, 1906; Randolph, 1952; Weatherwax, 1918). This theory has been ably supported in recent years by Weatherwax (1935, 1950), who has specialized in studies of the comparative morphology of the *Maydeae*, *Andropogoneae*, and other grasses, and favors the view of Vavilov (1931, 1950) that corn originated in Mexico or Central America. Evidence that in my opinion constitutes incontrovertible proof of the correctness of this view has just appeared from the fossil record, which previously has failed to make any significant contributions to the solution of this problem.

9. *The Discovery of Fossil Corn Pollen at Mexico City*

Probably the most significant discovery relating to the origin of corn that has been made since the establishment of the affinity of *Euchlaena* and *Tripsacum* to *Zea* by Ascherson in 1875 and the rediscovery of these wild relatives of corn in Mexico and Guatemala nearly a quarter of a century ago, was revealed in a publication by Barghoorn, Wolfe, and Clisby (1954) as the preparation of this article was nearing completion.

This discovery is of fossil pollen of *Zea*, *Euchlaena*, and *Tripsacum*, so well-preserved and beautifully prepared for cytological examination, and so closely resembling the pollen of the living plants, that there can be no question about their identification. These pollen grains were secured at the site of the Belles Artes museum near the present center of Mexico City. The most ancient samples of corn pollen came from a depth of more than 200 feet and are estimated on the basis of glacial chronology to be at least 60,000 years old.

Fortunately, the very large size of the grains in comparison to those of other grasses, and the relatively smooth exine facilitated the identification of the pollen as belonging to the genus *Zea*. There are significant differences in certain dimensions of the pollen of *Zea*, *Tripsacum*, and *Euchlaena* which provided a means of distinguishing the grains of these three genera. The ratio of germ pore diameter to longitudinal dimension of the pollen grain was found to be significantly different for the three species. Preparations of both living and fossil grains were made by the same technique to provide an accurate comparison and were preserved as glycerine jelly mounts. Although relatively few grains were recovered, the numbers were sufficient in most cases, and their identification sufficiently unequivocal to substantiate the interpretations placed upon them.

Fossil grains closely resembling the pollen of living corn were secured from upper levels of the cores ranging to a depth of 6 m. No

estimates of the age of these fossil grains were given, but it was stated that the larger ones presumably are of cultivated corn. Three smaller grains identified as *tripsacum* pollen and three of intermediate size provisionally identified as *teosinte* pollen were secured from these same levels. An additional *tripsacum* grain was obtained from a depth of 45 m. and three more from a depth of about 74 m., but no *teosinte* pollen was found at levels below 3.6 m.

The most significant discovery of Barghoorn, Wolfe, and Clisby (1954) were the large grains very similar to modern corn recovered from much lower depths of 69 and 70 m. A total of 19 grains which could be measured accurately were secured from this level. The authors concluded that these oldest fossil grains of corn pollen almost certainly antedate the practice of agriculture in North America and probably preceded the advent of man on this continent.

The photographs of the fossil pollen show very clearly the shape of the grains, the germ pore and surrounding annulus and the thickness of the exine. The characteristic folding of the grains as they collapse with the application of pressure or as a result of dessication is also shown in the photomicrographs. No one who is familiar with the appearance of fresh samples of corn pollen will question the identification of the fossil grains.

The discovery of fossil pollen supplements the archeological discoveries of prehistoric corn in New Mexico (Mangelsdorf and Smith, 1949), where the recovery of well-preserved ears and kernels from dry caves proved the existence of a primitive maize culture in that area dating from approximately 1000 A.D. to nearly 4000 B.C. Since the fossil corn pollen antedates this material by many thousands of years and belongs to a period much earlier than that of the earliest known records of man on the North American continent, it must have come from a wild species of *Zea*, of which there might well have been several at this early period in the evolutionary history of the genus.

Although the dimensions of the most ancient fossil corn pollen studied by Barghoorn, Wolfe, and Clisby were similar to those of most varieties of modern corn which they examined, this does not necessarily mean that they belong to the same species. Since the pollen measurements for different species in the allied genus *Tripsacum* are very similar, the possibility exists that the fossil corn pollen is not that of *Zea mays* but of an extinct species of *Zea*, which had pollen of essentially the same size as that of *Zea mays*. The diversity of existing races of cultivated corn, especially with respect to chromosome morphology, genetic variability, and ecological adaptation, suggests that more than one species of *Zea* might have been involved in their origin.

Perhaps the most significant aspect of the discovery of fossil corn pollen in Mexico is that it proves beyond any reasonable question of doubt that corn was indigenous to this general region, which is at the present time the primary center of diversity of the *Maydeae*. However, this discovery does not necessarily prove that cultivated corn originated in this area. It is possible that various wild species of *Zea* indistinguishable by pollen analysis were widely distributed in this early period. If so, more than one of these species might have been domesticated, possibly at different times, and in different places, and served as progenitors of modern varieties of corn. Obviously, the evidence available at the present time can be interpreted in favor of the view that the species to which this pollen belonged, or one very much like it, was the progenitor of modern maize, and that domestication took place in this general area. But other possibilities should not be ignored.

Of special interest in this connection are the archeological discoveries by Junius Bird (1948) and other investigators (Ford, 1954) of an established premaize agriculture in southern Peru, which was followed by the advent of maize into the area along with Cupisnique pottery some 2500 years ago. This is understandable if cultivated corn originated in Central America or elsewhere to the north at a much earlier period and later spread southward.

10. Summary ✓

Recent advances in the cytogenetics of corn and its relatives have contributed to a better understanding of their evolutionary history. The natural relationships existing among the members of the tribe *Maydeae* to which corn belongs are better understood as a result of studies on the number, form, and synaptic behavior of the chromosomes in *Zea*, *Euchlaena*, *Tripsacum*, and other more distantly related genera. Conspicuous numerical and structural differences in their chromosomes separate all known species of *Tripsacum* and cultivated varieties of corn, which are difficult or impossible to cross. Corn and teosinte, which cross readily and produce fertile progeny, have chromosomes which are very similar in appearance, synaptic behavior, and genic composition. Conclusions concerning the manner and place of origin of corn drawn from cytogenetic studies recently have received strong support from archeological and paleobotanical research. We do not yet know how corn originated, but we do know that wild corn was indigenous to central Mexico many thousands of years ago.

Both corn and teosinte have 10 chromosomes in their germ cells; some species of *Tripsacum* have 18 and others 36. A species of *Manisuris* which is found in the southwestern United States and Mexico and

is very similar to the more grasslike species of *Tripsacum* has 9 chromosomes in its germ cells. There are species of *Coix* and *Sorghum* with 5 chromosomes, but neither the morphology of their chromosomes nor their geographic distribution favors the assumption that corn originated as an amphidiploid of such species. The evidence from duplicate genes concerning the possible amphidiploid origin of corn is equally unconvincing.

From studies of chromosome morphology and pairing at pachytene and later stages of meiosis it has been shown that the chromosomes of corn and teosinte are very similar in length, centromere positions, and regularity of synaptic association; those of *tripsacum* are much shorter on the average, have different arm ratios and very pronounced differences in appearance, and synapse very rarely with corn chromosomes.

Chromosome knobs which occur in fixed positions on the pachytene chromosomes occupy terminal positions on the chromosomes of *tripsacum* and Guatemalan teosinte; in corn and Mexican teosinte they are mostly intercalary. Knobs are lacking or few in number in flint and flour corn of the northeastern United States, in the Andean corn of South America, and among high-altitude races of northwestern Guatemala. Knobs are more numerous in the Indian corn of the southwestern United States and at the lower altitudes of Guatemala and Mexico. Corn Belt corn and most South American corn on the average have intermediate knob numbers. A total of 22 knob positions have been identified in corn.

Natural hybrids of corn and teosinte occur in Mexico and Guatemala, but have never been reported for corn and *tripsacum* or for teosinte and *tripsacum*. Hybrids of teosinte and corn are highly fertile and crossing over occurs with normal frequency in such hybrids except for genes in the short arm of chromosome 9. Hybrids of corn and *Tripsacum dactyloides* may be obtained readily with special techniques; races of corn and species of *Tripsacum* in Guatemala and Mexico are highly cross-incompatible. Experimental hybrids of corn and *Tripsacum dactyloides* are highly sterile, their chromosomes rarely synapse regularly, and in backcrosses to corn the *tripsacum* chromosomes disappear rapidly. The transfer of a terminal knob from a *tripsacum* chromosome to a knobless corn chromosome produced no associated phenotypic effect. Attempts to obtain teosinte-like plants in progenies of corn-*tripsacum* hybrids have not been successful.

The extent to which hybridization of corn with teosinte and *tripsacum* has contributed to corn improvement is an open question. There is very little cytogenetic evidence of such admixtures of germ plasm. Structural uniformity of the chromosomes in varieties of corn from

widely separated localities in the United States, Central America, and South America and the regularity of synaptic association in corn-teosinte hybrids are proof of the absence of inversions, translocations, or other alterations in chromosome morphology ordinarily involved in species crosses. Mutation and selection offer a simpler explanation of the variability that is characteristic of cultivated varieties of corn.

Recent archeological and paleobotanical discoveries have demonstrated conclusively that cultivated corn has been in existence in the southwestern United States for at least 3000 years and that wild corn was indigenous to central Mexico.

REFERENCES

- ANDERSON, E. G. 1938. Translocations in maize involving chromosome 9. *Genetics* **23**: 307-313.
- ANDERSON, E. 1945. What is *Zea mays*? A report of progress. *Chron. Bot.* **9**: 88-92.
- ANDERSON, E., and BROWN, W. L. 1952. Origin of corn belt maize and its genetic significance. In "Heterosis." Iowa State College Press, Ames, Iowa.
- ANDERSON, E., and ERICKSON, R. O. 1941. Antithetical dominance in North American maize. *Proc. Natl. Acad. Sci. U. S.* **27**: 436-440.
- ANDERSON, E. G., and RANDOLPH, L. F. 1945. Location of centromeres on the linkage maps of maize. *Genetics* **30**: 518-526.
- ARNASON, T. J. 1936. Cytogenetics of hybrids between *Zea Mays* and *Euchlaena mexicana*. *Genetics* **21**: 40-60.
- ARNOLD, J. R., and LIBBY, W. F. 1951. Radiocarbon dates. *Science* **113**: 111-120.
- ASCHERSON, P. 1880. Bemerkungen über ästigen Maiskolben. *Bot. Ver. Prov. Bran.* **21**: 133-138.
- AZARA, FELIX DE. 1809. "Voyages dans l'Amérique Méridionale (1781-1801)." Walckenaer, Paris.
- BARGHOORN, E. S., WOLFE, M. K., and CLISBY, K. H. 1954. Fossil maize from the valley of Mexico. *Botan. Museum Leaflets Harvard Univ.* **16**: 229-240.
- BEADLE, G. W. 1932. The relation of crossing over to chromosome association in *Zea-Euchlaena* hybrids. *Genetics* **17**: 481-501.
- BEADLE, G. W., 1939. Teosinte and the origin of maize. *J. Heredity* **30**: 245-247.
- BIRD, J. B. 1948. Preceramic cultures in Chicama and Virú. *Am. Antiquity* **13**: 21-28.
- BONAFOUS, M. 1836. "Histoire naturelle, agricole et économique du maïs." Huzard, Paris.
- BREMER, G. 1923. A cytological investigation of some species and species hybrids within the genus *Saccharum*. *Genetica* **5**: 97, 274.
- BRIDGES, C. B. 1938. A revised map of the salivary gland x-chromosome. *J. Heredity* **29**: 11-13.
- BRIEGER, F. G. 1944. Estudos experimentais sobre a origem do milho. *Anais escola super. agr. "Luiz de Queiroz," Univ. São Paulo*, Sep. **10**: 225-278.
- BROWN, R. W. 1934. The supposed fossil ear of maize from Cuzco, Peru. *J. Wash. Acad. Sci.* **24**: 293-296.
- BROWN, W. L. 1949. Numbers and distribution of chromosome knobs in U. S. maize. *Genetics* **34**: 524-536.
- CLISBY, K. H. 1954. Studies of Mexican profiles. 2. Pollen profiles. *Bull. Am. Geol. Soc.* (in press).

- COLLINS, G. N. 1909. A new type of Indian corn from China. *Bur. Plant Ind. Bull.* 161.
- COLLINS, G. N. 1912. The origin of maize. *J. Wash. Acad. Sci.* 2: 520-530.
- COLLINS, G. N. 1919. A fossil ear of maize. *J. Heredity* 10: 170-172.
- COOPER, D. C., and BRINK, R. A. 1937. Chromosome homology in races of maize from different geographic regions. *Am. Naturalist* 71: 582-587.
- CUTLER, H. C. 1944. Medicine men and the preservation of a relict gene in maize. *J. Heredity* 35: 290-294.
- CUTLER, H. C. 1951. The oldest corn in the world. *Chicago Natural History Museum Bull.* 22: 4-5.
- CUTLER, H. C., and ANDERSON, E. 1941. A preliminary survey of the genus *Tripsacum*. *Ann. Missouri Botan. Garden* 28: 249-269.
- DECANDOLLE, A. 1884. "Origin of cultivated plants." Kegan Paul, Trench & Company, London.
- EMERSON, R. A., and BEADLE, G. W. 1932. Studies of *Euchlaena* and its hybrids with *Zea*. II. Crossing-over between the chromosomes of *Euchlaena* and those of *Zea*. *Z. ind. Abstam.-u. Vererbungslehre* 62: 305-315.
- EMERSON, R. A., BEADLE, G. W., and FRASER, A. C. 1935. A summary of linkage studies in maize. *Cornell Univ. Agr. Expt. Sta. Mem. No.* 180: 1-83.
- FARQUHARSON, L. I. 1953. Peculiarities in the embryology of *Tripsacum dactyloides*. *Indiana Acad. Sci. Proc.* 62: 104.
- FARQUHARSON, L. I. 1954a. Natural selection of tetraploids in a mixed colony of *Tripsacum dactyloides*. *Indiana Acad. Sci. Proc.* 63: 80-82.
- FARQUHARSON, L. I. 1954b. Apomixis, polyembryony and related problems in *Tripsacum*. Ph. D. Thesis, Indiana University.
- FORD, J. A. 1954. The history of a Peruvian valley. *Sci. American* 191: 28-34.
- GANN, T., and THOMPSON, J. E. 1931. "The History of the Maya." Scribners, New York.
- GARBER, E. D. 1947. The pachytene chromosome of *Sorghum intrans*. *J. Heredity* 38: 251.
- GOODWIN, A. J. H. 1953. The origin of maize. *S. African Arch. Bull.* 8: 13, 14.
- GRANER, E. A., and ADDISON, G. 1944. Meiose em *Tripsacum australe* Cutler e Anderson. *Anais escola super. agr. "Luiz de Queiroz," Univ. São Paulo*, Sep. 9: 213-224.
- HARSHBERGER, J. W. 1893. Maize, a botanical and economic study. *Contr. Botan. Lab. Univ. Pa.* 1: 75-202.
- HARSHBERGER, J. W. 1896. Fertile crosses of teosinthe and maize. *Garden and Forest* 9: 522, 523.
- HERNANDEZ-XOLOCOTZI, E., and RANDOLPH, L. F. 1950. Descripción de los *Tripsacum* diploides de México: *Tripsacum maizar* y *Tripsacum zopilotense* spp. nov. *Ofic. Estud. Esp. Sec. Agr. y Ganad. Fol. tec. No.* 4: 1-28.
- HITCHCOCK, A. S. 1922. A perennial species of teosinte. *J. Wash. Acad. Sci.* 12: 205-208.
- ILTIS, H. 1911. Über einige bei *Zea Mays* L. beobachtete Atavismen. *Z. ind. Abstam.-u. Vererbungslehre* 5: 38-57.
- JANAKI-AMMAL, E. K. 1939. *Current Sci. (India)* 8: 210. (Cited by Darlington, C. D., and Janaki-Ammal, E. K. 1945. In "Chromosome Atlas of Cultivated Plants," London.)
- JANAKI-AMMAL, E. K. 1940. Chromosome diminution in a plant. *Nature* 146: 839.
- JANAKI-AMMAL, E. K. 1941. Intergeneric hybrids of *Saccharum*. *J. Genet.* 41: 217-253.

- KEMPTON, J. H., and POPENOE, W. 1937. Teosinte in Guatemala. *Carnegie Inst. Wash. Publ.* **483**: 199–218.
- KUWADA, Y. 1915. Über die chromosomenzahl von *Zea Mays* L. *Botan. Mag. (Tokyo)* **29**: 83–89.
- KUWADA, Y. 1919. Die chromosomenzahl von *Zea Mays* L. *J. Coll. Sci. Imp. Univ. Tokyo* **39**: 1–148.
- LANGHAM, D. G. 1940. The inheritance of intergeneric differences in *Zea-Euchlaena* hybrids. *Genetics* **25**: 88–107.
- LAUGHNAN, J. R. 1949. The action of allelic forms of the gene *A* in maize II. The relation of crossing over to mutation of *A^b*. *Proc. Natl. Acad. Sci. U. S.* **35**: 167–178.
- LAUGHNAN, J. R. 1952a. On the designation of closely linked genes with similar effects. *Am. Naturalist* **86**: 109.
- LAUGHNAN, J. R. 1952b. The *A^b* components as members of a duplication in maize. *Genetics* **37**: 598.
- LEWIS, E. B. 1945. The relation of repeats to position effect in *Drosophila melanogaster*. *Genetics* **30**: 137–166.
- LIMA-DE-FARIA, A. 1949. The structure of the centromere of the chromosomes of rye. *Hereditas* **35**: 77–85.
- LIMA-DE-FARIA, A. 1952. Chromosome analysis of the chromosome complement of rye. *Chromosoma* **5**: 1–68.
- LI, H. W., MA, T. H., and SHANG, K. C. 1954. *Taiwan-Sugar* **1**: 13–24.
- LINDSTROM, E. W. 1925. Heritable characters of maize 21. A new dominant hereditary character Teopod. *J. Heredity* **16**: 135–140.
- LONGLEY, A. E. 1924. Chromosomes in maize and maize relatives. *J. Agr. Research* **28**: 673–682.
- LONGLEY, A. E. 1932. Chromosomes in grass sorghums. *J. Agr. Research* **44**: 317.
- LONGLEY, A. E. 1934. Chromosomes in hybrids between *Euchlaena perennis* and *Zea Mays*. *J. Agr. Research* **48**: 789–806.
- LONGLEY, A. E. 1937. Morphological characters of teosinte chromosomes. *J. Agr. Research* **54**: 836–862.
- LONGLEY, A. E. 1938. Chromosomes of maize from North American Indians. *J. Agr. Research* **56**: 177–195.
- LONGLEY, A. E. 1939. Knob positions on corn chromosomes. *J. Agr. Research* **59**: 475–490.
- LONGLEY, A. E. 1941a. Knob positions on teosinte chromosomes. *J. Agr. Research* **62**: 401–413.
- LONGLEY, A. E. 1941b. Chromosome morphology in maize and its relatives. *Botan. Rev.* **7**: 263–289.
- LONGLEY, A. E. 1952. Chromosome morphology in maize and its relatives. *Botan. Rev.* **18**: 399–412.
- MAGUIRE, M. P. 1952. Synapsis and crossing over of *Tripsacum* and *Zea* chromosomes derived from hybrids backcrossed to *Zea*. Thesis, pp. 1–104. Cornell University, Ithaca, New York.
- MANGELSDORF, P. C. 1947. The origin and evolution of maize, *Advances in Genet.* **1**: 161–207.
- MANGELSDORF, P. C. 1952. Hybridization in the evolution of maize. In "Heterosis." Iowa State College Press, Ames, Iowa: 175–198.
- MANGELSDORF, P. C. 1954. New evidence on the origin and ancestry of maize. *Am. Antiquity* **19**: 409–410.

- MANGELSDORF, P. C., and CAMERON, J. W. 1942. Western Guatemala a secondary center of origin of cultivated maize varieties. *Botan. Museum Leaflets, Harvard Univ.* **10**: 217-252.
- MANGELSDORF, P. C., and REEVES, R. G. 1931. Hybridization of maize, *Tripsacum* and *Euchlaena*. *J. Heredity* **22**: 329-343.
- MANGELSDORF, P. C., and REEVES, R. G. 1935. A trigeneric hybrid of *Zea*, *Tripsacum*, and *Euchlaena*. *J. Heredity* **26**: 129-140.
- MANGELSDORF, P. C., and REEVES, R. G. 1938. The origin of maize. *Proc. Natl. Acad. Sci. U. S.* **24**: 303-312.
- MANGELSDORF, P. C., and REEVES, R. G. 1939. The origin of Indian corn and its relatives. *Texas Agr. Expt. Sta. Bull.* **574**: 1-315.
- MANGELSDORF, P. C., and REEVES, R. G. 1945. The origin of maize: present status of the problem. *Am. Anthropologist* **47**: 235-243.
- MANGELSDORF, P. C., and SMITH, C. E. 1949. New archaeological evidence on evolution in maize. *Botan. Museum Leaflets Harvard Univ.* **13**: 213-247.
- McCLINTOCK, B. 1930. A cytological demonstration of the location of an interchange between non-homologous chromosomes of *Zea Mays*. *Proc. Natl. Acad. Sci. U. S.* **16**: 791-796.
- MONTGOMERY, E. G. 1906. What is an ear of corn? *Popular Sci. Monthly* **68**: 55-62.
- MULLER, H. J. 1939. Genetics in the scheme of things. *Proc. 8th Intern. Congr. Genet. Stockholm*, pp. 96-127.
- O'MARA, J. G. 1942. A cytogenetic study of *Zea* and *Euchlaena*. *Missouri Agr. Expt. Sta. Research Bull.* **341**: 1-16.
- PARODI, L. 1946. Los especies de *Sorghum* cultivadas en la Argentina. *Rev. argentina agron.* **13**: 1-35.
- RANDOLPH, L. F. 1928. Types of supernumerary chromosomes in maize. *Anat. Record* **41**, 102.
- RANDOLPH, L. F. 1932. Some effects of high temperature on polyploidy and other variations in maize. *Proc. Natl. Acad. Sci.* **18**: 222-229.
- RANDOLPH, L. F. 1945. Embryo culture of *Iris* seed. *Bull. Am. Iris Soc.* **97**: 33-45.
- RANDOLPH, L. F. 1950. Crossability of maize and *Tripsacum* in relation to theories of the origin of maize. *Proc. VII Intern. Botan. Congr. Stockholm*, pp. 179-180.
- RANDOLPH, L. F. 1952. New evidence on the origin of maize. *Am. Naturalist* **86**: 193-202.
- RANDOLPH, L. F., and HERNANDEZ-XOLOCOTZI, E. 1947. The discovery of a diploid *Tripsacum* in Mexico. *Am. J. Botany* **34**: 588.
- RANDOLPH, L. F., and HERNANDEZ-XOLOCOTZI, E. 1950. Cytotaxonomic diversity of *Tripsacum* in Mexico. *Genetics* **35**: 686.
- RANDOLPH, L. F., and McCLINTOCK, B. 1926. Polyploidy in *Zea Mays* L. *Am. Naturalist* **60**: 99.
- REEVES, R. G. 1944. Chromosome knobs in relation to the origin of maize. *Genetics* **29**: 141-147.
- REEVES, R. G. 1953. New "evidence" on the origin of maize. *Am. Naturalist* **87**: 157-159.
- REEVES, R. G., and MANGELSDORF, P. C. 1935. Chromosome numbers in relatives of *Zea Mays* L. *Am. Naturalist* **69**: 633-635.
- REEVES, R. G., and MANGELSDORF, P. C. 1942. A proposed taxonomic change in the tribe Maydeae (family Gramineae). *Am. J. Botany* **29**: 815-817.
- RHOADES, M. M. 1945. On the genetic control of mutability in maize. *Proc. Natl. Acad. Sci. U. S.* **31**: 91-95.
- RHOADES, M. M. 1951. Duplicate genes in maize. *Am. Naturalist* **85**: 105-110.

- RHOADES, M. M. 1952. Preferential segregation in maize. In "Heterosis," pp. 66-80. Iowa State College Press, Ames, Iowa.
- RHOADES, M. M., and DEMPSEY, E. 1953. Cytogenetic effects of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. *Am. J. Botany* **40**: 405-424.
- SCHWEINFURTH, G. 1904. Das älteste Herbarium der Welt. *Vossische Zeitung*. November 25.
- SINGLETON, W. R. 1951. Inheritance of corn grass a macromutation in maize, and its possible significance as an ancestral type. *Am. Naturalist* **85**: 81-96.
- SPRAGUE, G. F. 1932. The inheritance of colored scutellums in maize. *U. S. Dept. Agr. Tech. Bull.* **292**: 1-43.
- STADLER, L. J., and FOGEL, S. 1945. Gene variability in maize. II. The action of certain R alleles. *Genetics* **30**: 23-24.
- STONOR, C. R., and ANDERSON, E. 1949. Maize among the hill peoples of Assam. *Ann. Missouri Botan. Garden* **36**: 355-404.
- SUTO, T. 1952. Genetic analysis of a mosaic pericarp in maize. *J. Fac. Sci. Hokkaido Imp. Univ. (Ser. V)* **6**: 69.
- SUTO, T. 1952. Analysis of polymeric genes controlling a new form of dotted leaves in maize. *J. Fac. Sci. Hokkaido Imp. Univ. (Ser. V)* **6**: 151.
- THOMPSON, E. H. 1932. "The People of the Serpent." Houghton Mifflin, New York.
- VACHHANI, N. V. 1950. A study of the relationship of chromosome knobs with certain agronomic and morphological characters in corn inbreds. *Agron. J.* **42**: 196-201.
- VAVILOV, N. I. 1931. Mexico and Central America as the principal centers of origin of cultivated plants of the New World. *Bull. Appl. Botany, Genet., Plant Breeding (Leningrad)* **26**: 135-200.
- VAVILOV, N. I. 1950. The origin, variation, immunity and breeding of cultivated plants (Transl. by K. S. Chester). *Chron. Botan.* **13**: 1-364.
- WEATHERWAX, P. 1918. The evolution of maize. *Bull. Torrey Botan. Club* **45**: 309-342.
- WEATHERWAX, P. 1926. Comparative morphology of the oriental Maydeae. *Indiana Univ. Studies* **73**.
- WEATHERWAX, P. 1935. The phylogeny of *Zea Mays*. *Am. Midland Naturalist* **16**: 1-71.
- WEATHERWAX, P. 1945. Early contacts of European science with the Indian corn plant. *Proc. Indiana Acad. Sci.* **54**: 169-178.
- WEATHERWAX, P. 1950. The history of corn. *Sci. Monthly* **71**: 50-60.
- WEATHERWAX, P. 1951. The first printed picture of Indian corn. *Proc. Indiana Acad. Sci.* **60**: 273-275.
- WEATHERWAX, P. 1954. "Indian Corn in Old America." The Macmillan Co., New York.

CHAPTER II

Vegetative Morphology

JOHN E. SASS

I. Development of the Caryopsis

1. Development of the Embryo

a. The Proembryo. The vegetative phase of the life of a maize plant begins with the zygote, which is derived by fusion of the egg and sperm, approximately 24 hours after pollination (Randolph, 1936). Division of the zygote occurs approximately 12 hours after fertilization (Randolph, 1936) and produces a two-celled proembryo with a transverse cell wall. The planes of subsequent cell divisions conform to the "asterad" type of proembryo development (Johansen, 1950). The term "proembryo" is used for stages prior to detectable organ initiation, and the term "embryo" for subsequent stages.

The clavate proembryo is at first externally symmetrical in longitudinal and transverse aspects; however, the internal cellular organization exhibits asymmetry by the fifth day. Localized acceleration of cell division produces an oblique zone of highly meristematic, deeply stainable cells, located on the distal-anterior end of the proembryo. This zone of activity foreshadows organ formation (Fig. 2).

b. Organogeny. External expression of organ formation consists of three lobes that are usually evident 10 days after pollination. The prominent "posterior lobe" gives rise to the mid-portion and proximal portion of the scutellum. The oblique "distal lobe" produces the distal extension of the scutellum. The "anterior lobe" gives rise to the plumular axis (Fig. 3). The orientation of the embryo in the caryopsis is shown in Fig. 1.

The coleoptile primordium arises immediately above the axial lobe, approximately 10 days after pollination (Fig. 4). In transverse section, the coleoptile primordium is at first a short, oblique crescent, which becomes a complete ring by progressive activation of cells under the ends of the crescent. This mode of initiation and growth is typical of the grass leaf.

The radicle primordium is usually well defined in the central region of the embryo by the 10th day (Fig. 5); however, specialized activity in

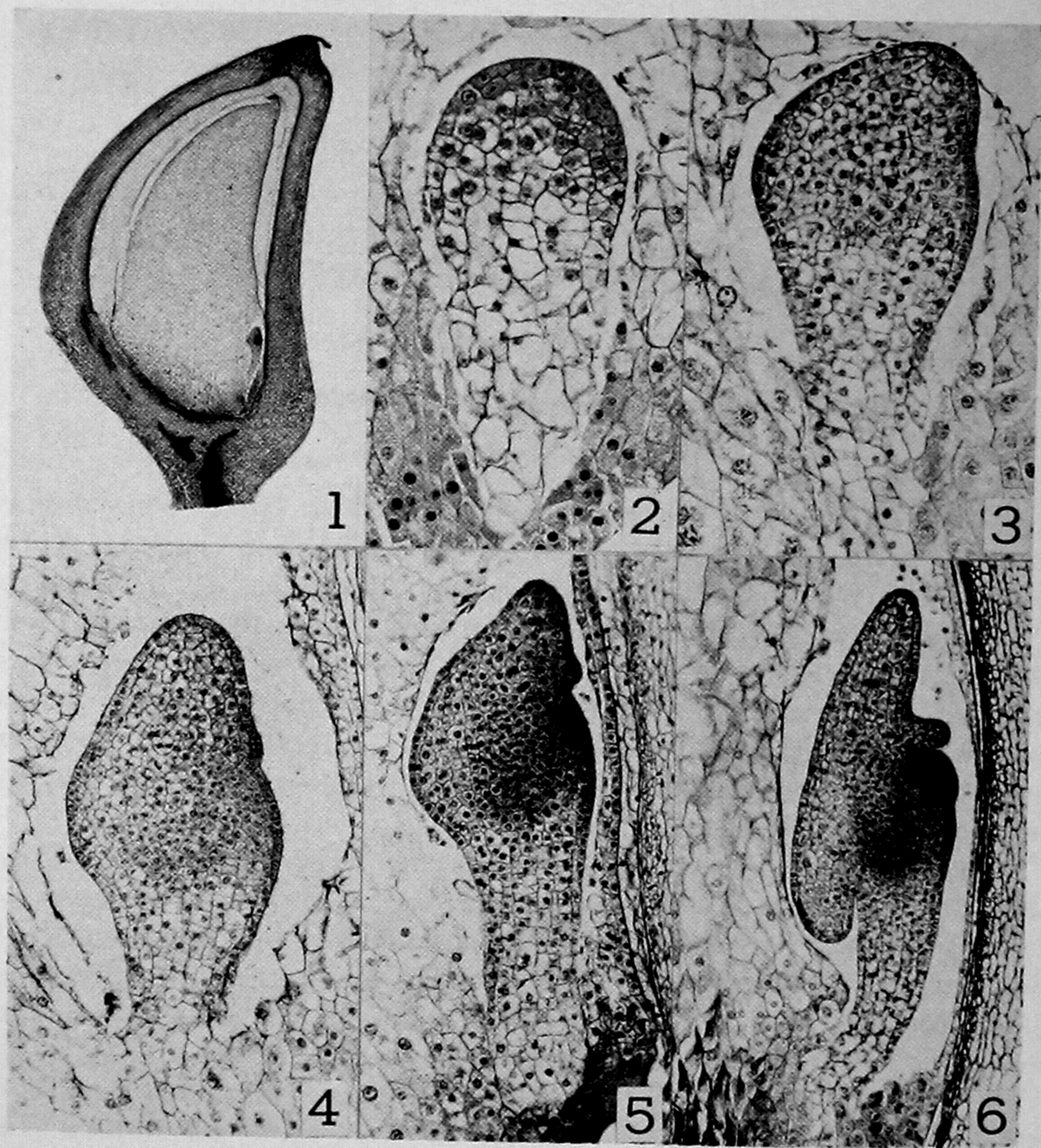


FIG. 1. Longitudinal section of kernel of pop corn, 10 days after pollination. 12X.
(Posterior lobe at left, anterior at right, distal toward top of page in Figs. 1-6.)

FIG. 2. Embryo of yellow dent corn, 5 days. 130X.

FIG. 3. Embryo of yellow dent corn, 10 days. 130X.

FIGS. 4, 5. Embryo of yellow dent corn, 10 days. 98X.

FIG. 6. Embryo of "smoky flint" corn, 10 days. 92X.

this zone can be detected as early as the 5th day. The planes of successive cell divisions comprise an arc, which eventually becomes the dome-shaped tip of the radicle.

On the basis of the foregoing criteria of organ initiation, it may be concluded that the embryonic organs, root, stem, coleoptile, and scutellum become clearly defined 10 days after pollination.

The primordium of the first foliage leaf is detectable by the 12th

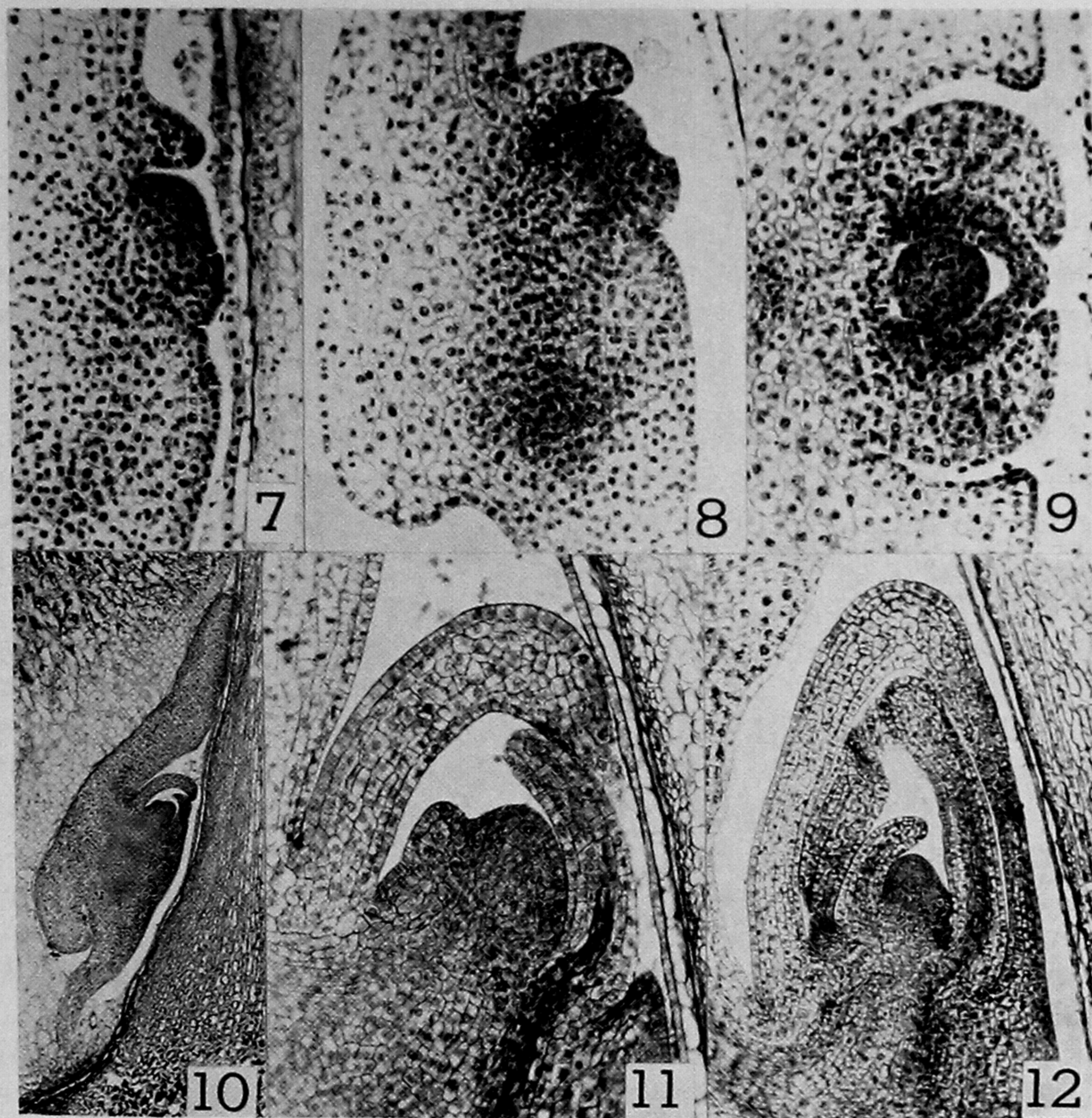


FIG. 7. Plumular primordia of "brittle" yellow dent corn, 12 days. 130 $\times$.

FIG. 8. Plumule-radicle axis of sweet corn, 12 days. 130 $\times$.

FIG. 9. Transverse section of plumular organs of waxy yellow dent corn, 12 days. 130 $\times$.

FIG. 10. Structurally normal, but retarded embryo of "germless" inbred line, 15 days. 31 $\times$.

FIG. 11. Detail of plumule of inbred sweet corn, 15 days. 130 $\times$.

FIG. 12. Plumule of yellow dent hybrid, 15 days. 66 $\times$.

day, as a protuberance on the anterior side of the plumular apex, opposite the coleoptile primordium (Figs. 8, 9). The first detectable activity that initiates leaf formation occurs in the surface layer, the tunica, followed immediately by cell division in the adjacent subsurface zone, the corpus (Sharman, 1942; Ledin, 1954).

In transverse section, the leaf primordium is a short crescent. Cell division in the apical dome under the ends of the crescent progresses

laterally until an annular meristematic ridge is formed. This ring produces the encircling, adnate base of the leaf (Fig. 9). The distal edge of the primordium produces the free, overlapping edges of the sheath, and also the blade of the leaf.

The second foliage leaf is initiated before the 15th day, on the side of the apical dome opposite the first leaf (Figs. 10, 11). By this time the blade of the first leaf usually encircles the stem, and the leaf edges meet or overlap (Fig. 14). The coleoptile becomes an oblique cone that encloses the plumular axis by the 15th day, except for a narrow vertical slit (Fig. 11).

The time of initiation of the third foliage leaf lags appreciably in inbred lines, many of which have only two foliage leaves at 15 days, or at most a zone of activity at the locus of initiation of the third leaf (Fig. 14), whereas many hybrids have three distinct leaves. The fourth leaf is usually present by the 20th day in some hybrids (Fig. 16), whereas many inbreds and some hybrids have only three leaves. The fifth and last embryonic leaf is commonly present 30 days after pollination (Fig. 17), and is almost invariably present before the 40th day in the numerous lines, hybrids, and varieties that have been examined (Fig. 18). Some weak inbreds have only a zone of activation at the locus of the fifth leaf.

The leaf blade expands by the activity of a continuous marginal meristem (Figs. 14, 15), and the edges of the older leaves overlap. Successive leaves attain progressively less overlapping, and the fifth leaf in the mature embryo is usually a short crescent.

In the inbred lines and hybrids that have been grown in central Iowa and studied in the writer's laboratory, the first foliage leaves are initiated earlier than in the corn described by Randolph (1936) and Kiesselbach (1949). Regional surveys of the developmental rates of adapted stocks, as well as the behavior of unadapted and exotic varieties, would provide useful information for genetic, physiological, and other studies. There is limited evidence that some very early, short varieties that have few foliage leaves at maturity, may prove to have fewer than five embryonic leaves. The exceedingly tall Central and South American types deserve further study to determine whether five is their maximum embryonic leaf number (Sass, 1951a).

Abbe and Stein (1954) described the dimensional changes of the shoot apex during embryonic plastochrones, the intervals between the initiation of successive leaves. The length and width of the apex increase during successive plastochrones, cell size remains constant, and cell number increases. The rate of leaf initiation is deceleratory during embryogeny, and acceleratory during seedling growth.

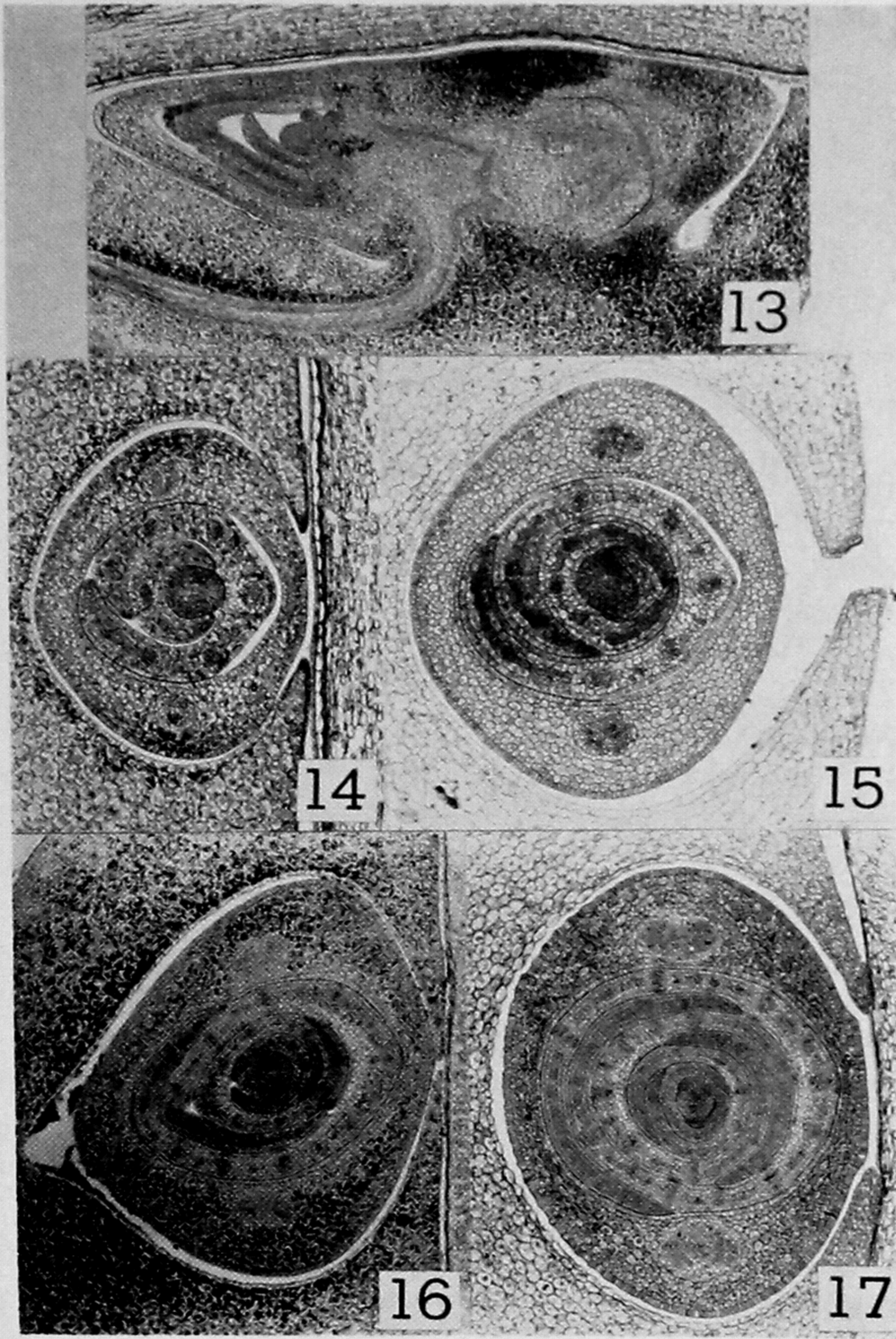


FIG. 13. Plumule-radicle axis of Iowax hybrid, 15 days. 32 $\times$.

FIG. 14. Transverse section of plumule of Iowax hybrid, 15 days. 66 $\times$.

FIG. 15. Plumule of yellow dent inbred, 20 days. 66 $\times$.

FIG. 16. Plumule of Iowax hybrid, 20 days, 40 $\times$.

FIG. 17. Plumule of yellow dent, 30 days. 40 $\times$.

The rate of initiation and development of embryonic leaves is sufficiently consistent under given conditions to be used in studies of heterosis (Groszmann and Sprague, 1948). Fairchild (1953) has shown that leaf development is faster in the embryos of certain crosses than in the inbred parents; however, at maturity, these inbreds as well as the hybrids have five embryonic leaves.

Leaf initiation and development in the numerous kernels on an ear were found by Bell (1954) to be remarkably uniform. This makes possible the use of a relatively small sample, from any part of the ear, for diagnostic or comparative purposes.

Vascularization in the plumule is well under way 15 days after pollination, when the two strands of the coleoptile and at least the median strand of the first foliage leaf are evident (Figs. 11, 14). As a leaf continues its lateral growth, procambium strands are initiated near the active edge (Figs. 15–18). The median strand is the first to exhibit differentiation of vascular elements. One protoxylem and one protophloem element can be unmistakably identified 20 days after pollination in vigorous hybrids. A comparable condition is not evident in some inbreds until 30 days. Very little further vascular differentiation occurs in the leaves. The oldest leaf bundle of the mature embryo has three or four protophloem sieve tubes, one thick-walled protoxylem element, and one or two enlarged, but thin-walled, nucleate protoxylem initials.

The two strands of the coleoptile enlarge by divisions of peripheral cells, and the compact arrangements and stainability of the cells defines the kidney-shaped strands sharply. Most of the numerous varieties that have been examined have no fully differentiated xylem cells in the coleoptile at maturity; however, a very early popcorn consistently has one or two fully differentiated, lignified protoxylem elements in each coleoptile bundle in the mature, dried grain.

The internode below the plumule, between the coleoptile node and the scutellar node, is a characteristic and unique feature of the Gramineae. The term "mesocotyl" has been used extensively in the literature to designate the first internode. This internode is not evident 15 days after pollination, when the coleoptile node is virtually in contact with the scutellar node (Fig. 13). Subsequent intercalary growth produces the long internode (Fig. 20).

Anatomically, most of the first internode in the embryonic axis resembles the root. The broad parenchymatous cortex and the stele are delimited by a poorly defined endodermis. The enlarged metaxylem initials of the exarch xylem can be identified with certainty in the stele (Fig. 22), but the other vascular elements do not become so obvious until after germination. Toward the distal end of the first internode, the vascular system undergoes transition to discrete collateral bundles scattered throughout the ground parenchyma. The first internode is inserted at the top of a long disc, the scutellar node. If the scutellum is regarded as the homologue of a cotyledon, all structures above the scutellar node comprise the epicotyl, and all structures below

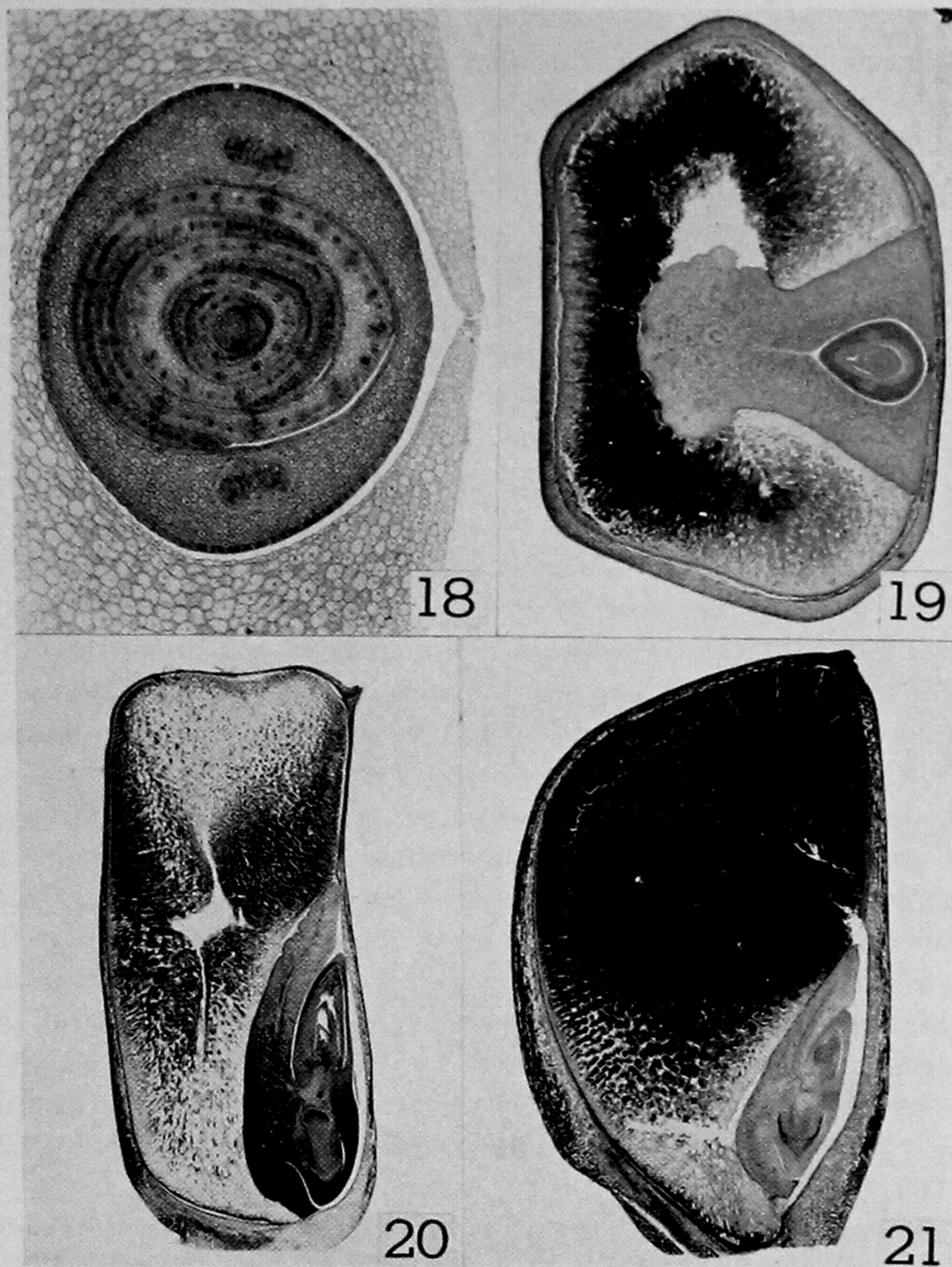


FIG. 18. Plumule of yellow dent single cross, 40 days. 41 $\times$. (From Fairchild, 1953.)

FIG. 19. Transverse section of kernel at level of stem tip, hybrid 939, 30 days. 8 $\times$.

FIG. 20. Longitudinal section of kernel of Iowax hybrid, 20 days. 5 $\times$.

FIG. 21. Longitudinal section of kernel of inbred white pop corn, 20 days. 9 $\times$.

the node are hypocotyl. The radicle and the associated coleorhiza would then comprise the hypocotyl.

The early initiation of the embryonic radicle has been mentioned briefly in a previous section. Cell division continues rapidly in the zone of radicle initiation, and a zone of cells in the form of a dome becomes well defined between the 10th and 15th day. Near the periphery of this

dome, a substance of unknown composition is deposited between the cell walls. This deposition, the dark-stained layer in Figs. 13, 21, and 23, is assumed to interrupt organic continuity between the adjacent cells, and a cleft appears before the 20th day. The cleft elongates during subsequent elongation of the radicle, and separates the radicle from the cylindrical coleorhiza (Figs. 20, 24). The cleavage does not extend across the tip of the radicle (Fig. 13); therefore, continuity of tissues between the root tip and the coleorhiza is maintained until germination.

A transverse, stratified zone of cells develops across the end of the radicle between the 15th and 20th day, and the calyptrogen is evident 20 days after pollination (Fig. 20).

Vascular development in the radicle begins 12 to 15 days after pollination. A central core, the future stele, becomes evident by virtue of the difference in cell size, cell orientation, and staining density in the stele, in contrast with the encasing cortex. Linear columns of metaxylem vessel initials become appreciably enlarged by 15 days (Fig. 13), and protoxylem initials are considerably enlarged by 30 days (Fig. 24). Protophloem does not become fully differentiated until germination (Picklum, 1953).

The scutellum is a distinctive organ that has neither the mode of origin nor mature structure of any other embryonic organ. A major part of the bulk of a 10-day embryo is tissue that will be incorporated into the scutellum (Fig. 4). The most rapid growth occurs at first in the distal lobe, but in 15 to 20 days the proximal lobe curves under the coleorhiza and ruptures the suspensor (Figs. 10, 13). Lateral growth of the edges of the scutellum is also very rapid. An active ridge arises on the anterior face by 12 days (Fig. 9), extends part way around the axis by 15 days (Fig. 14), and completely encloses the axis by 20 days (Fig. 16).

A median procambium strand is barely detectable in the scutellum of weaker inbreds by 15 days (Fig. 10), whereas vigorous hybrids have a large, well-developed strand extending far into the distal lobe at 15 days (Fig. 13). Minor lateral procambium strands ramify irregularly into the distal portion of the scutellum. The proximal lobe of the scutellum has a few strands that extend only a short distance below the scutellar node. Differentiated vascular elements have not been found in the scutellar strands in the mature kernel.

The surface cell-layer of the scutellum has been studied and discussed by various authors in relation to the enzyme-secreting and food-absorbing function of the scutellum. The "epidermal" cells are elongated anticlinically, and they have dense, deeply stainable protoplasm. In some lines of corn the surface of the scutellum is smooth,

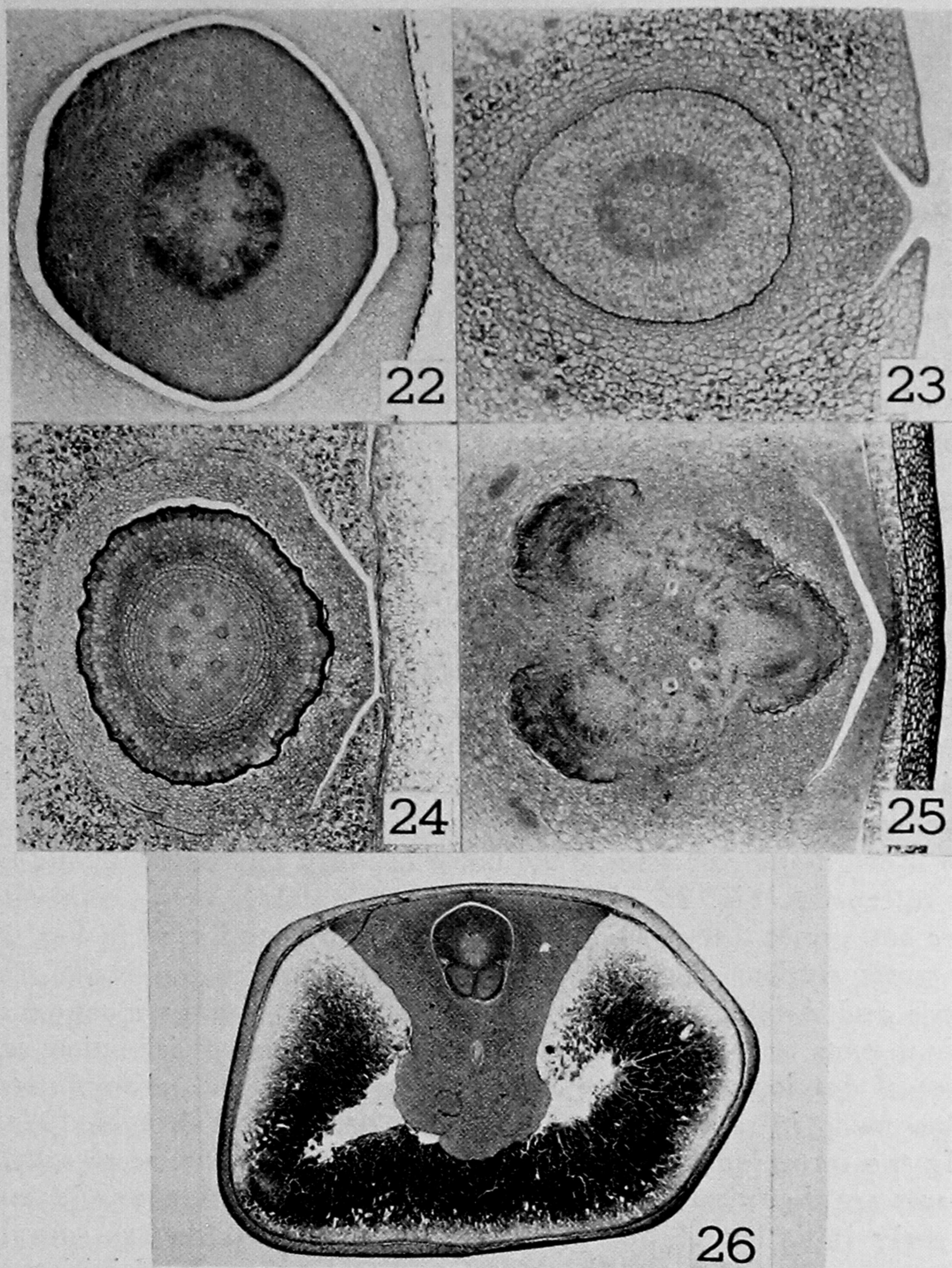


FIG. 22. Transverse section of first internode (mesocotyl) of dry mature kernel, yellow dent. 31 $\times$.

FIG. 23. Transverse section of radicle in embryo of yellow dent inbred Os420, 20 days. 65 $\times$.

FIG. 24. Transverse section of radicle and coleorhiza of yellow dent. 30 days. 39 $\times$.

FIG. 25. Section through seminal roots of yellow dent hybrid 939, 30 days. 31 $\times$.

FIG. 26. Transverse section of kernel of hybrid 939, at base of first internode, 35 days. 8 $\times$.

Considerable starch is evident in the endosperm approximately 12 days after pollination, a little earlier in pop corn than in dent corn. Younger kernels have large plastids in the endosperm, but the starch does not give a convincing color test with iodine. Starch does not accumulate in sufficient quantities for the iodine test until the endosperm has filled the nucellar space.

The polarizing microscope reveals starch grains that are too small to detect with iodine. The characteristic appearance of starch by polarized light is shown best by grains in regions of the kernel in which the grains are not tightly packed in the cells (Fig. 28). The narrow,

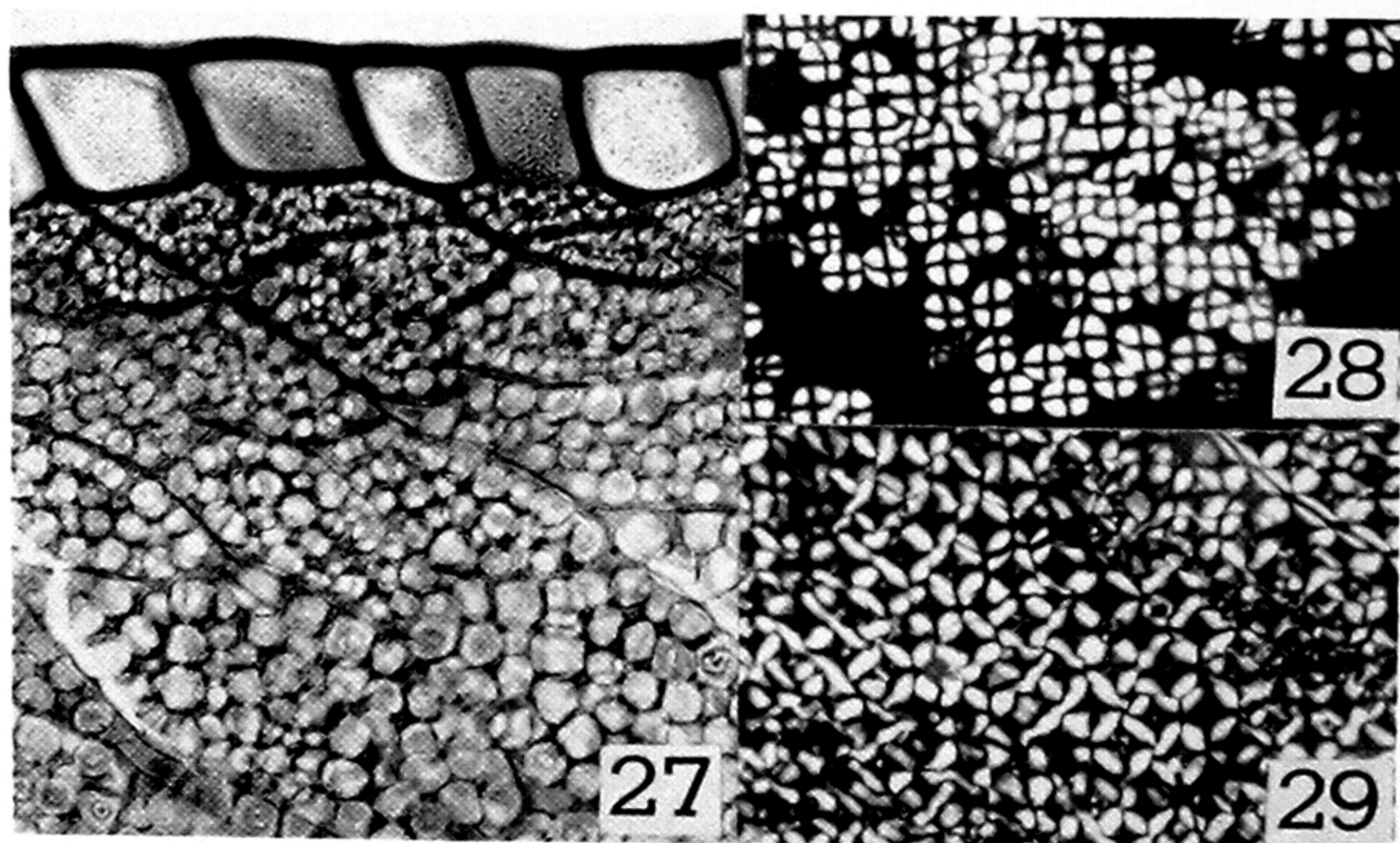


FIG. 27. Detail of endosperm starch and aleurone of yellow dent, at level of scutellar tip, 35 days. 280X.

FIG. 28. Starch by polarized light, near base of kernel of pop corn, 35 days. 280X.

FIG. 29. Starch by polarized light, at stylar end of kernel of pop corn, 35 days. 280X.

dark central cross rotates as the analyzer is rotated. A strikingly different pattern is evident in grains that are tightly packed, as in the distal region of the pop corn kernel, or at the level of the scutellar tip in dent corn (Figs. 27, 29). This change in the relationship between the light and dark zones suggests a change in the structure of the "compressed" granules.

The pattern of starch distribution in the kernel becomes well established in 15 to 20 days. The numerous kinds of maize fall into two types with respect to this pattern. In flint and pop corn, the starch is most densely packed in the stylar region, and the density tapers off toward the base (Fig. 21). In dent corn, the zone of greatest density is in the form of an open cylinder that partly encircles the embryo (Figs. 19, 20).

II. Histology of the Vegetative Plant Body

1. Cytology of Germination

Germination of the kernel follows an orderly pattern of biochemical and morphological processes. Bernstein (1943) and Toole (1924) have described the mobilization and movement of food reserves during germination. Picklum (1953) studied imbibition of water by the kernel and the cytology of germination. He demonstrated that water enters primarily through the pericarp, and to a lesser degree through the fractured pedicel. The cells of the coleorhiza and radicle tip are the first to become turgid. Linear growth of cells of the coleorhiza pulls the coleorhiza away from the root cap (Fig. 30), and the elongating coleorhiza emerges. Subsequently, mitosis and cell elongation begin in the radicle, approximately 24 hours after the beginning of imbibition. Within 48 hours after the emergence of the primary root, the primordia of the lateral roots may become evident.

Mitosis begins in regions of the embryo in the following sequence: Midway between the root tip and the scutellar plate, progressing toward the tip; the cortex at the base of the first internode (mesocotyl); the base of the coleoptile; the leaf margins; the stem tip. Emergence of the plumule and its elevation to the surface of the soil occur mainly by the activity of the meristematic zone below the coleoptile node. Picklum (1953) found that under the specified conditions postembryonic leaves were initiated at 60-hour intervals.

During germination, the chromatin stains more deeply in the epithelial cells of the scutellum than in the internal cells, but no other cytological changes occur in the epithelial cells. The parenchymatous cells within the scutellum are uninucleate prior to germination. During germination, the nuclei become deeply lobed, and the lobes may become abstricted, forming multinucleate cells.

The pericarp over the scutellar node is ruptured by the expansion of a cushion-like mass of tissue on the anterior side (Fig. 31). Pressure exerted by the elongating first plumular internode may be a minor factor in rupturing the pericarp. The histological development of the plumule and radicle are described in subsequent sections.

2. The Stem

a. The Apical Meristem. The stem apex, which is initiated on the anterior face of the proembryo approximately 10 days after pollination, maintains structural and functional continuity as a vegetative apex until the tassel primordium is initiated. The shoot apex of the seedling,

like that of the embryo, has a single surface layer of cells, the tunica, in which the planes of cell division are almost exclusively anticlinal. The second layer structurally resembles the tunica in some apices, but in other apices, especially very active ones, the second layer has many

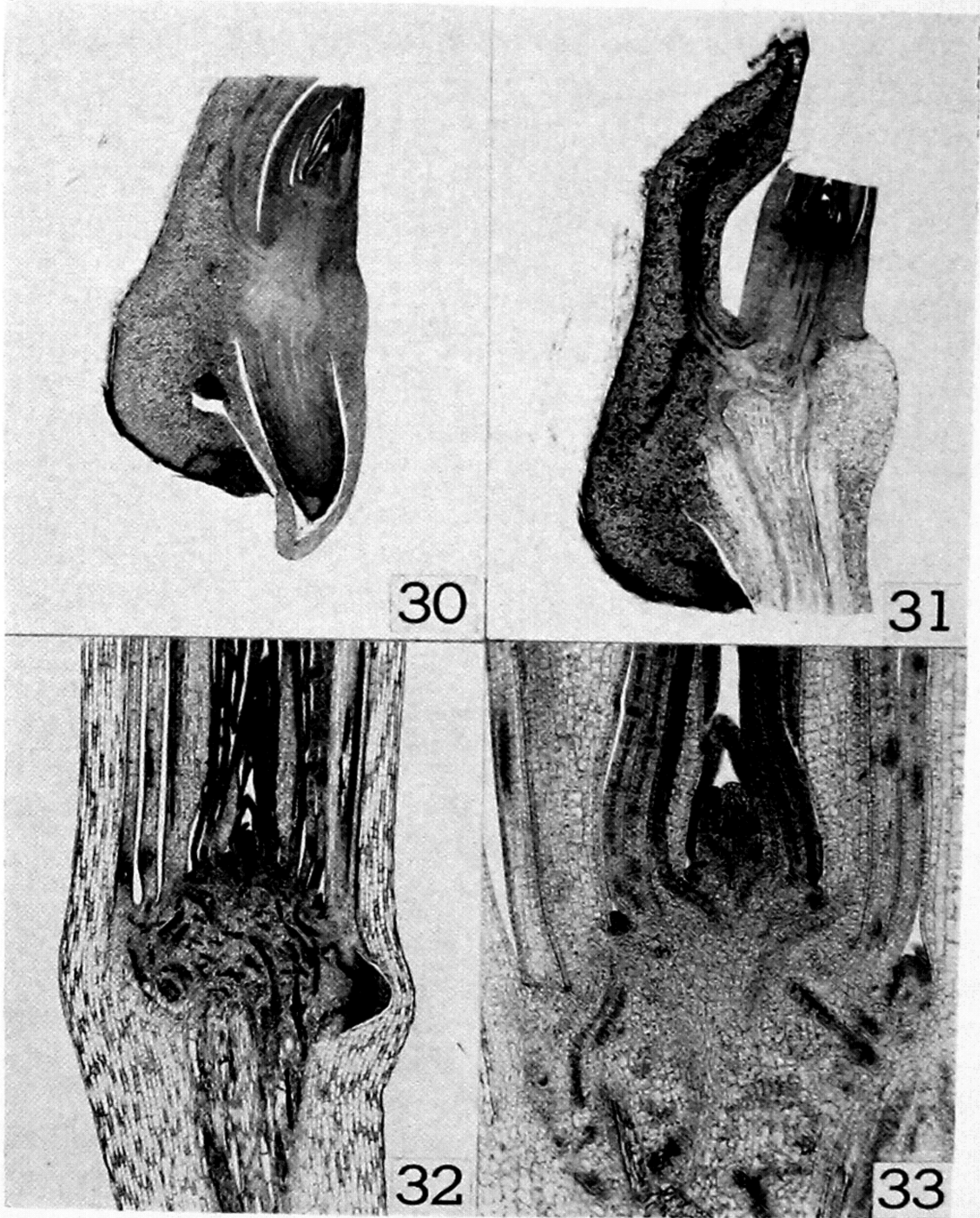


FIG. 30. Embryo of yellow dent corn, 24 hours after beginning of imbibition. 7 $\times$. (From Picklum, 1953.)

FIG. 31. Portion of embryo after 36 hours. 7 $\times$. (From Picklum, 1953.)

FIG. 32. Plumule at coleoptile node, 96 hours. 13 $\times$. (From Picklum, 1953.)

FIG. 33. Longitudinal section of seedling stem, 1 week after emergence above soil level. 40 $\times$.

periclinal as well as anticlinal divisions. Such activity is intermediate between that of the tunica and the more or less random planes of division in the central corpus. The danger of rigid designations of meristematic zonation is evident.

b. Organogeny. The formation of foliage leaves on the stem apex is resumed soon after the onset of germination (Fig. 32). The factors that incite this reactivation and control the rate of leaf initiation will require further study. The mechanism of leaf formation on the seedling apex appears to be the same as on the embryonic apex. The process is terminated by a transition phase, which leads to the initiation of the inflorescence (Bonnet, 1953, Leng, 1951).

Axillary bud primordia arise very early in stem ontogeny, near the base of the third or fourth leaf below the tip. The primordium actually arises in the internode above the subtending leaf. These axillary primordia become vegetative tillers near the base of the plant, and potential ear shoots at the upper levels.

c. Histogenesis. The structure of the histogens of the stem apex has been reviewed by Bonnet (1953). The derivation of tissue systems will be outlined here. Procambium can be detected in the stem axis of maize at the approximate level of the second leaf primordium below the tip. Strands arise from ground meristem cells, which in turn are derived from corpus cells of the apex. It is possible that a strand arises from a single vertical column of cells, but such derivation is difficult to demonstrate because a strand can not be identified with certainty until it consists of 4 to 6 cells in transverse aspect, and after these cells have undergone some vertical elongation (Fig. 33). The individual procambial cell is an elongated prismatic cell with relatively dense cytoplasm and a large, elongated nucleus. The strand increases in diameter by longitudinal cell division. The tissue in which the strands are encased is best designated residual meristem (Esau, 1943), in which cell division occurs with decreasing frequency as the stem matures. Most of this tissue differentiates into the interfascicular "pith" parenchyma of the mature stem.

The differentiation of the procambium strand into a vascular bundle has been described in detail by Sharman (1942) and Esau (1943). The unique stainability of the first protophloem element makes this cell readily distinguishable very early in the ontogeny of the bundle (Fig. 34). The first protoxylem element becomes evident soon thereafter (Fig. 35). It is possible that further development of staining and optical techniques may show that protophloem and protoxylem arise essentially simultaneously in the strand.

The first xylem element is an annular trachea, also known as a tracheal tube, or vessel. Before this xylem element has become mature, a centrifugally adjacent column of procambium cells begins to enlarge. These cells also develop into a protoxylem trachea. Similarly, two or more tracheae develop progressively in centrifugal sequence (Fig. 36).

The first and second tracheae invariably have annular secondary wall thickenings. Subsequent tracheae may be annular or spiral protoxylem tracheae. A vessel segment can have both annular and spiral thickenings. The bundles toward the periphery of the stem, which become

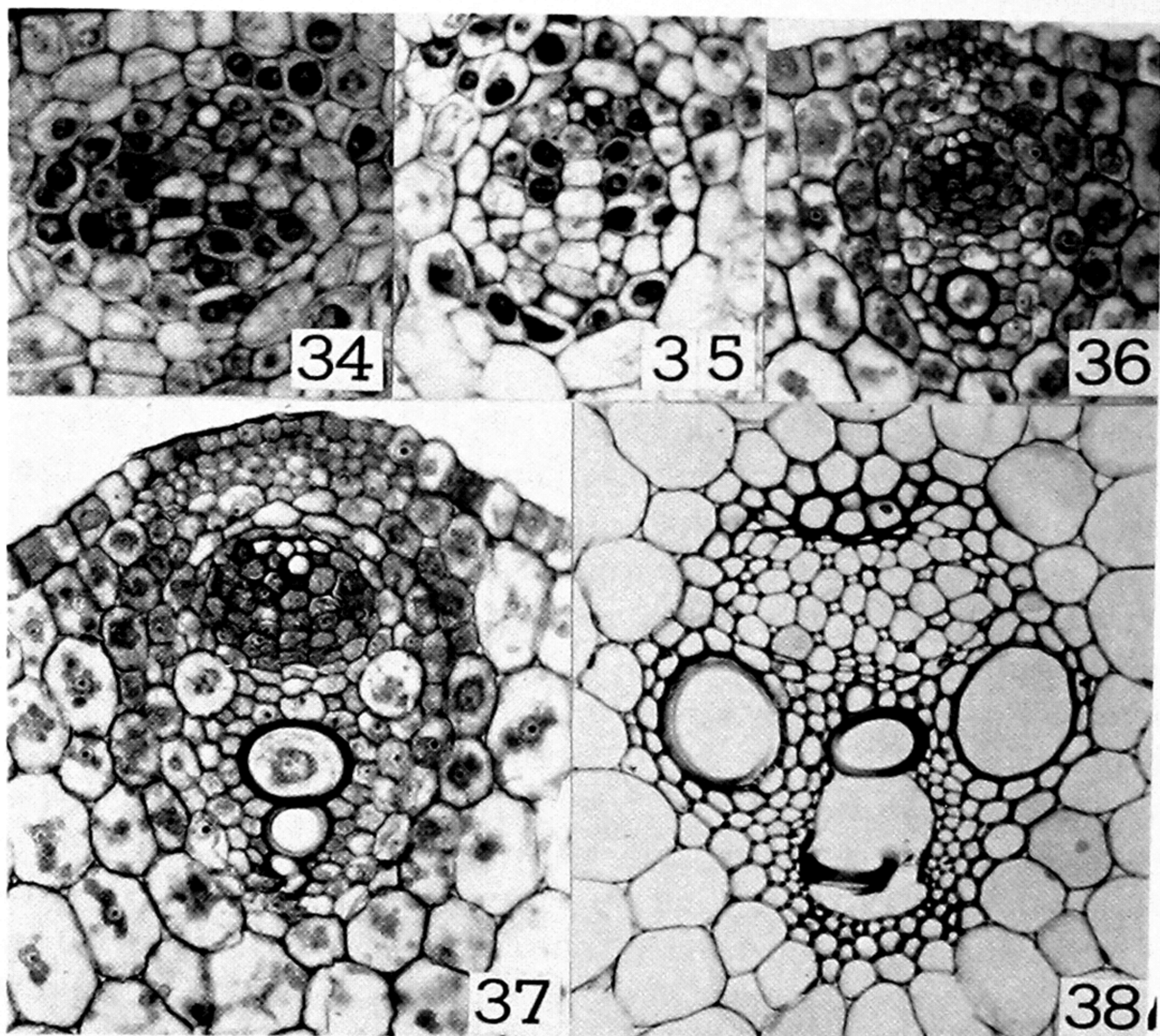


FIG. 34. Procambium strand with 1 protophloem sieve tube. 490 $\times$. (From Esau, 1943.)

FIG. 35. Procambium strand with two protophloem sieve tubes and one mature protoxylem element. 490 $\times$. (From Esau, 1943.)

FIG. 36. Developing vascular bundle with group of sieve tubes, cambiform layer, and differentiating xylem elements. 260 $\times$.

FIG. 37. Vascular bundle with enlarged metaxylem vessels and cambiform zone. 260 $\times$.

FIG. 38. Bundle of central region of stem of stiff-stalked synthetic. 198 $\times$.

mature after a given level of the stem has ceased elongation, do not have spiral tracheae, and may have little or no protoxylem (Sass, 1951b).

A zone of cells external to the outermost protoxylem goes through a short period of cambiform activity and produces a zone of stratified derivatives (Fig. 37). Cell division is not limited to a single layer, and the useful but figurative term "cambiform" does not imply homology with the vascular cambium of dicotyledonous plants. On the lateral

edges of this zone, two procambial cells undergo rapid enlargement (Fig. 37) and develop into pitted metaxylem tracheae, the most prominent elements in the vascular bundle in grasses. Dissolution of the end walls of the original cells produces a continuous tube with "porous" ends between the segments. The side walls of these metaxylem tubes are profusely pitted. The spirally arranged pits may be so close and numerous that the wall is literally a reticulum. The inner derivatives of the afore-mentioned cambiform zone, between the large metaxylem vessels, differentiate into metaxylem elements. These cells are prismatic in three-dimensional aspect, and their transverse or slightly oblique end walls have several large pits, forming a reticulate end. Esau (1943) uses the term "tracheary elements" for these cells. The term "trachea" would not be inappropriate, but the term "tracheid" is not valid.

During the period of rapid elongation and increase in diameter of the young stem, the first-formed protoxylem elements, the annular and spiral tracheae, become stretched beyond the limit of elasticity of the primary wall. The cells become ruptured and the annular and spiral thickenings become dislodged. Several ruptured vessels merge into an irregular vertical cavity, the protoxylem lacuna (Fig. 38). This cavity probably contains standing water that contributes little or nothing to the transpiration stream.

A zone of cells on each side of the protoxylem remains relatively undifferentiated during the life of the bundle. These thin-walled, nucleate cells may be regarded as xylem parenchyma, of obscure function (Fig. 38). The ontogeny of the diverse components of the xylem has been reviewed here with unbroken continuity, and the phloem will be discussed in a similar manner.

The remarkably early differentiation of the first protophloem sieve tube is now widely recognized. Several more sieve tubes develop rapidly, without the formation of companion cells. The protophloem sieve tubes are enucleate when mature. The outer derivatives of cell division in the cambiform zone in the bundle develop into metaphloem. Each phloem initial cell divides longitudinally and produces a sieve tube and a companion cell. Esau (1943) has shown that the orderly pattern of the metaphloem is the result of derivation from the tangentially dividing cells of the cambiform zone of procambium. During the differentiation of the metaphloem, the protophloem becomes progressively compressed and almost obliterated. In the mature bundle the crushed protophloem persists as an irregular layer of stainable material (Fig. 38).

The peripheral cells of a developing vascular bundle continue to

divide and elongate during the period of internodal elongation. After the cessation of elongation, these cells differentiate into a sclerenchymatous sheath that encases the vascular bundle (Fig. 39). A typical mature sheath cell is hexagonal in section and the small lumen is circu-

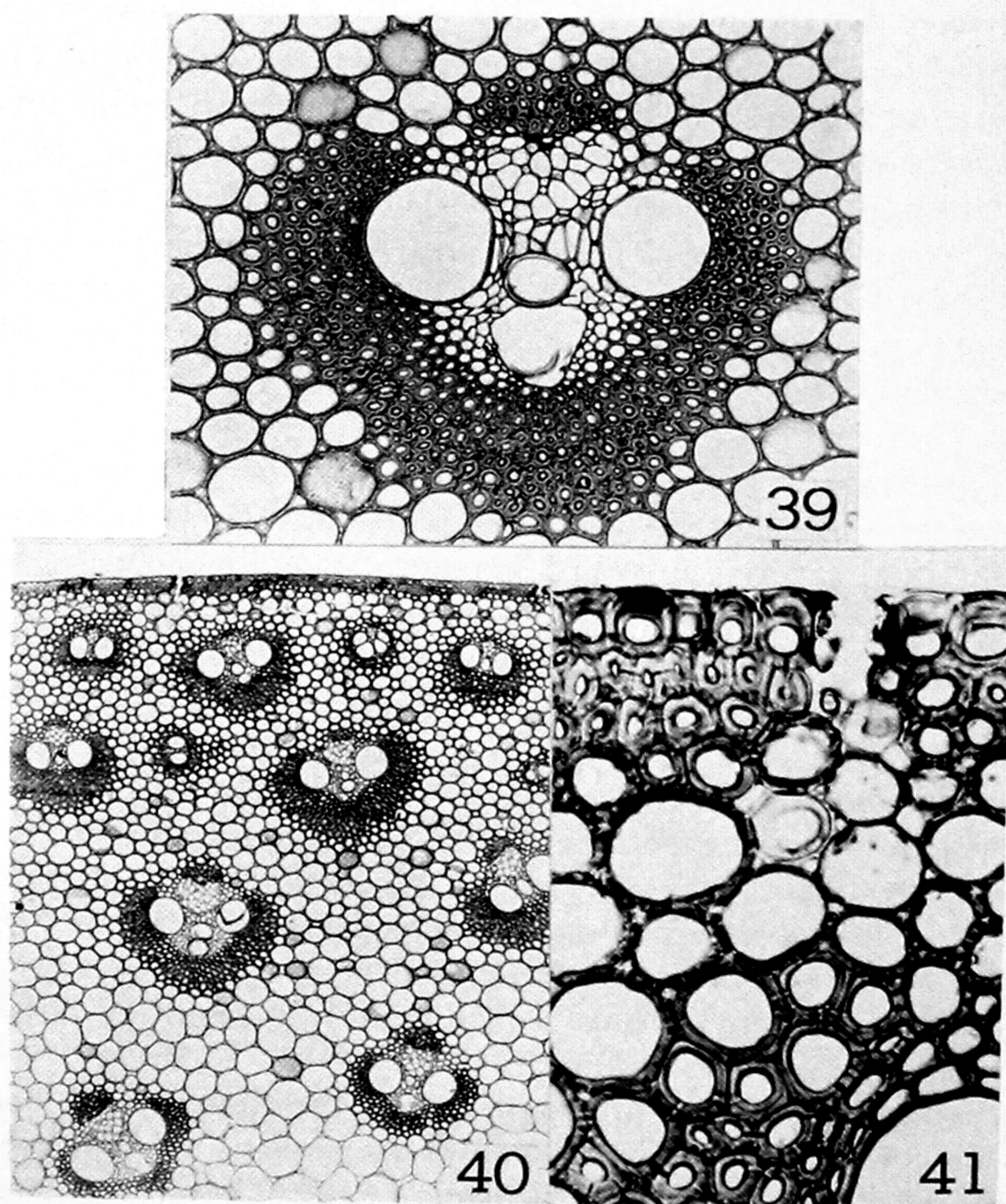


FIG. 39. Peripheral vascular bundle of stiff-stalked synthetic. 134X.

FIG. 40. Pattern of bundle distribution near periphery of stem of stiff-stalked synthetic. 40X.

FIG. 41. Detail on periphery of stem of stiff-stalked corn. 350X.

lar in section. The thick, laminated, lignified wall is sparsely pitted. The cell length is at least 50 times the diameter, and the cell ends are slightly oblique.

The peripheral bundles of the stem have wider sheaths than the bundles toward the center (Fig. 39). Bundle shape is fairly constant in the lines and hybrids that have been studied, and some lines have strikingly distinctive bundle shape.

The tissue between bundles in the center of the stem is typical "pith" parenchyma. The cells are large, the thin cellulose walls give a cellulose reaction, and large intercellular spaces are present (Fig. 38). The cytoplasm is a thin film around the large central vacuole.

Outward from the center of the stem, the parenchyma cells are progressively smaller and the intercellular spaces are also smaller. In this transitional zone the cells resemble collenchyma, as pointed out by Esau (1943). The cell walls become thicker as the periphery of the stem is approached, until a zone is reached in which the interfascicular cells are typical sclerenchyma (Fig. 40). The hypodermal zone is especially strikingly sclerified. The epidermal cells are small in transverse section, and the walls are greatly thickened. Sunken stomates occur in the linear pattern that is typical in grasses (Fig. 41). Chlorenchyma is present in the hypodermis, in the region of the stomates.

The zone of cells that includes the epidermis and extends inward through the sclerified parenchyma has been designated the "rind," for lack of a better term. This zone is of particular interest in relation to stalk stiffness, to lodging resistance, and possibly to resistance to insect and fungal damage. Magee (1948) has shown that a high percentage of sheath per bundle and a wide sclerified peripheral zone are correlated with stalk stiffness.

3. The Root

a. Histogenesis in the Apical Meristem. The early differentiation of the apical meristem of the radicle has been described in the section on embryology. The apical histogens become well defined long before the kernel is mature, and remain structurally constant during the subsequent emergence and growth of the root. The outermost histogen or tissue-generating zone is the calyptragen, a single, transverse, saucer-shaped layer of cells from which the root cap is derived. Some cell division occurs in the stratified derivatives of the calyptragen. The outermost region of the root cap becomes spongy, and the cells eventually slough away (Fig. 42). Continuous replacement occurs by activity of the calyptragen.

The second generating layer, located immediately behind the calyptragen, consists of the dermatogen-periblem initials. This transverse layer, one cell thick and three to five cells wide, can be identified by activity rather than by structural differentiation. The cells in the central region of the layer divide in anticlinal planes, parallel to the axis of the root. The marginal cells divide periclinally, tangential to the domed apex. The outer derivatives of this division divide almost exclusively anticlinally and thereby maintain the continuity and identity

of a surface layer. The term "dermatogen" may be applied to this surface layer, which ultimately becomes the hair-producing epidermis.

The inner derivatives of the dermatogen-periblem initials give rise to the cortex. These derivatives undergo numerous periclinal divisions and thereby broaden the periblem, a zone that represents a transitional phase in the development of the cortex. The inner zone of the periblem is particularly active, producing a stratified zone by tangential divisions that may well be designated "cambiform" activity (Figs. 42, 43). With the cessation of this activity, the innermost cell layer becomes the immature endodermis, the inner limiting layer of the cortex (Fig. 45).

The third generating layer of the root tip, located immediately behind the dermatogen-periblem initials, consists of a single layer of cells, the plerome initials, which give rise to the entire plerome, a transitional phase in the development of the stele. However, evidence is accumulating that the concept of the plerome as a transitional phase is losing its validity, because vascular elements are known to arise almost immediately from the generating initials. As shown in connection with the development of the radicle in the young embryo, linear columns of metaxylem initials can be traced almost to the tip of the radicle (Figs. 42, 43). In favorable preparations of the emerged radicle, the metaxylem columns can be traced to the second or third cell behind the plerome initials. Phloem cells are difficult to identify in longitudinal sections of root tips. In transverse sections near the tip, it is easy to identify proto-phloem sieve tubes, in immediate contact with the pericycle. The latter is a single layer of cells adjacent to the endodermis (Fig. 45).

Vascular elements are differentiated centripetally. The first proto-phloem cell, in contact with the pericycle, is a sieve tube, which arises directly from a histogen cell without the formation of a companion cell. Two or more protophloem tubes arise successively in a similar manner. This is followed by the differentiation of metaphloem, which consists of sieve tubes and companion cells. A sieve tube and its companion cell are sister cells, derived from a histogen cell. The protophloem is not appreciably crushed during the development of the metaphloem, but the latter comprises the major part of the phloem. The functional longevity of the protophloem is not known. The mature phloem is in the form of strands, alternating with the xylem arcs (Fig. 46).

Protoxylem elements become distinguishable much later than proto-phloem or metaxylem. The first protoxylem cells are in contact with the pericycle. Successive xylem cells arise centripetally and go through the enlargement phase progressively. The thickening and lignification of walls then begins in the outermost element and progresses inward. Thus, it is clear that the large innermost elements of the xylem, which

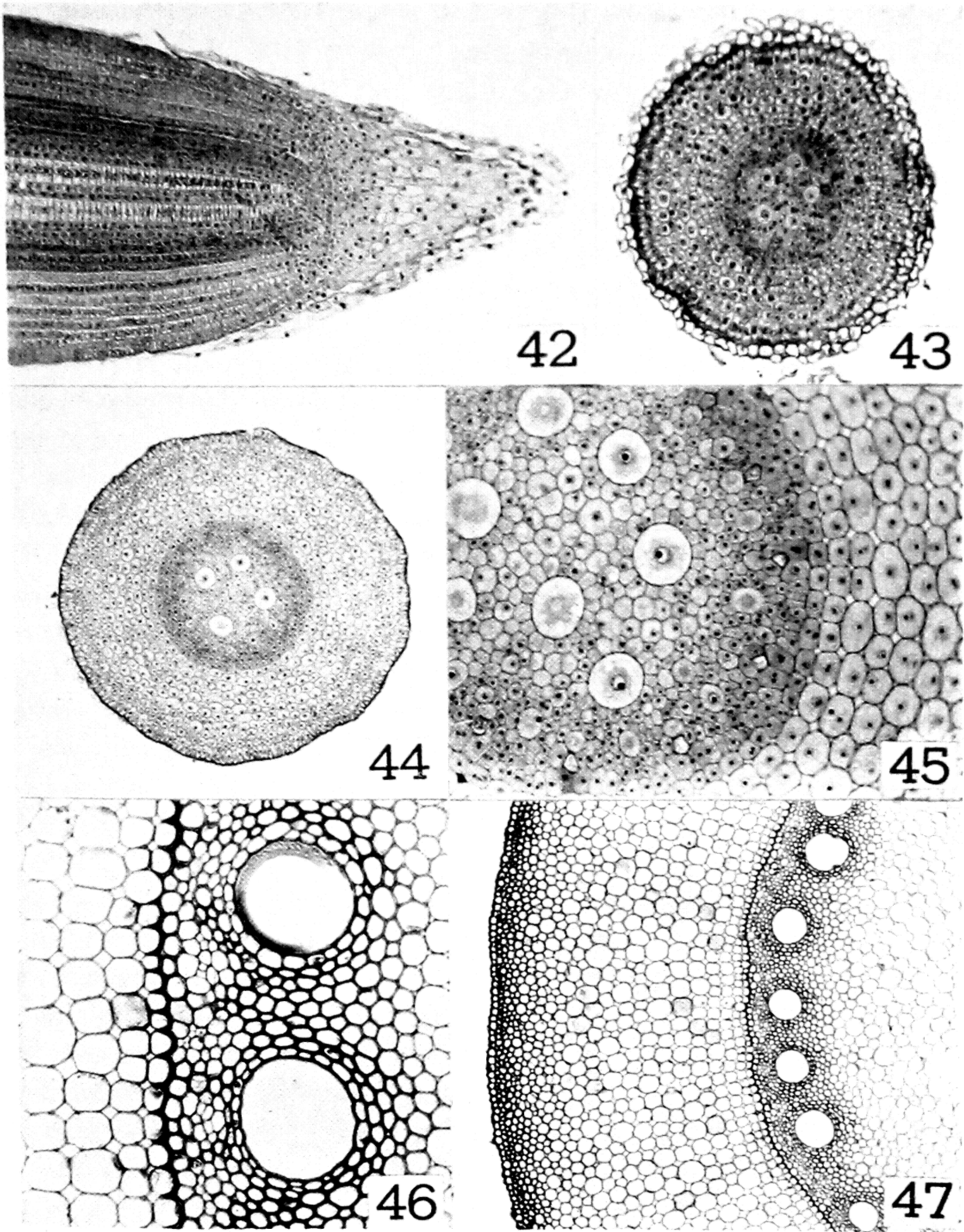


FIG. 42. Longitudinal section of root tip. 63 $\times$.

FIG. 43. Transverse section of root near tip, in zone of active cell division. 78 $\times$.

FIG. 44. Transverse section in zone where cell division has ceased and tissue differentiation has begun. 78 $\times$.

FIG. 45. Detail at stele-cortex interface of immature root. 130 $\times$.

FIG. 46. Detail at stele-cortex interface of root with fully differentiated tissues. 120 $\times$.

FIG. 47. Mature root showing all tissues from epidermis to pith. 40 $\times$.

begin to enlarge almost at the root tip, are the last to become structurally mature, and are therefore metaxylem (Fig. 47).

A zone of cells between the xylem and phloem has poorly understood affinities. The cells are small in diameter, closely packed, and have thick, lignified, pitted walls. The cells are structurally identical to the cells on the radial and inner sides of the metaxylem. A critical study of the derivation and pitting of the nontracheal lignified elements may clarify the affinities of such cells (Fig. 46).

The central tissue of the root is largely parenchymatous. The peripheral zone merges progressively into the previously mentioned lignified cells, whereas the nucleate central cells are loosely packed and have thin, cellulose walls. The term "pith" is a convenient designation for the parenchymatous central tissue.

Returning to the development of the cortex, it will be recalled that the maximum number of layers of cells in the cortex is established within a few millimeters of the root tip. The cell walls of the endodermis become thickened and lignified, and intercellular spaces develop between the enlarging, radially stratified cortical parenchyma (Fig. 46). At the upper limits of the root hair zone, the epidermal hairs and one or more layers of hypodermal parenchyma begin to collapse, and several layers of closely fitted subepidermal cells develop thick, lignified walls. This tough hypodermal sclerenchyma becomes the permanent protective layer of the root (Fig. 47).

b. Organogeny. The place, time, and manner of initiation of lateral organs of the root differs strikingly from the course of events in the stem. The meristematic potential of the pericycle of the root is well known. Lateral roots emerge a considerable distance from the tip, at a level where the differentiation of vascular tissues is well advanced; however, the place of initiation is much nearer the tip. The locus of initiation is the pericycle, opposite the protoxylem "points." The histogens of the lateral root become organized before the root has grown halfway through the cortex. The structure of the histogens and of the derivative tissues is identical in a lateral root and in the root from which it arose. Vascular differentiation occurs first in the lateral root at its base, establishes vascular continuity with the original root, and progresses distally.

4. The Leaf

a. Derivation and Histogenesis. The intimate relationship between the stem apex and leaf initiation made it desirable to describe leaf initiation in a previous section. After the encircling base of the leaf becomes established, the highly meristematic distal edge of the leaf primordium

produces the free edges of the blade. Continued activity of the marginal meristem of the leaf broadens the leaf, and the edges soon overlap (Fig. 14). The edge consists of a single row of cells. The number of cell layers increases rapidly, and the maximum number is attained a short distance from the edges (Fig. 15). In the surface layers, cell division parallel to the surface ceases approximately three cells from the edge, thereby establishing the identity and continuity of the "dermatogen," which becomes the epidermis. Anticlinal divisions continue in the surface cells, associated with the increase of leaf area. Increase in leaf thickness occurs thereafter by increase in the depth of epidermal cells, as well as by enlargement of the mesophyll cells, which become highly spongy (Fig. 49).

Procambium strands can be identified approximately 10 cells from the leaf margin. Strands arise from the meristematic mesophyll near the leaf edge. The differentiation of the major bundles of the blade is identical with the process in stem bundles, and the same pattern of vascular tissues occurs at maturity; however, the sheath of these major leaf bundles is distinctive. On the upper and lower sides of the bundle, a strand of sclerenchyma extends lengthwise of the leaf, in contact with the epidermis (Fig. 49). The sheath cells along the sides of the bundle have thickened and lignified inner walls. This is suggestive of endodermis, but the cells contain large chloroplasts, most of which are against the outer wall.

A second type of leaf bundle lacks the annular and spiral protoxylem elements and the two large metaxylem vessels. These bundles have only a few metaxylem and metaphloem elements. The prominent bundle sheath consists of large thin-walled cells that contain large chloroplasts, mostly against the outer wall. These bundles lack the strands of sclerenchyma, and thus are completely enveloped in the spongy parenchyma of the mesophyll. Relatively few blade bundles are structurally intermediate between the major and minor bundle types.

In the midrib and in the adjacent blade the bundles are close to the lower surface. Most of the bundles are of the major type, anchored to the lower epidermis by sclerenchyma (Fig. 48). The mesophyll of the rib consists of thin-walled, polygonal, closely fitted parenchyma with few chloroplasts.

During the differentiation of the lower epidermis, the cells enlarge to approximately uniform size, except in the vicinity of the stomates. The upper epidermis develops a pattern that is characteristic of the grasses. The cells adjacent to the stomates are small in transverse section. Cell size increases progressively away from a stomate, reaches a

maximum, and then becomes smaller to the next stoma (Fig. 49). The large epidermal cells are the bulliform or motor cells. Their change of turgor in relation to water supply and transpiration is associated with the curling and uncurling of the leaf blade.

The surface view of the epidermis conforms to the well-known pattern of the grass leaf (Fig. 50). The stomates occur in rows extending

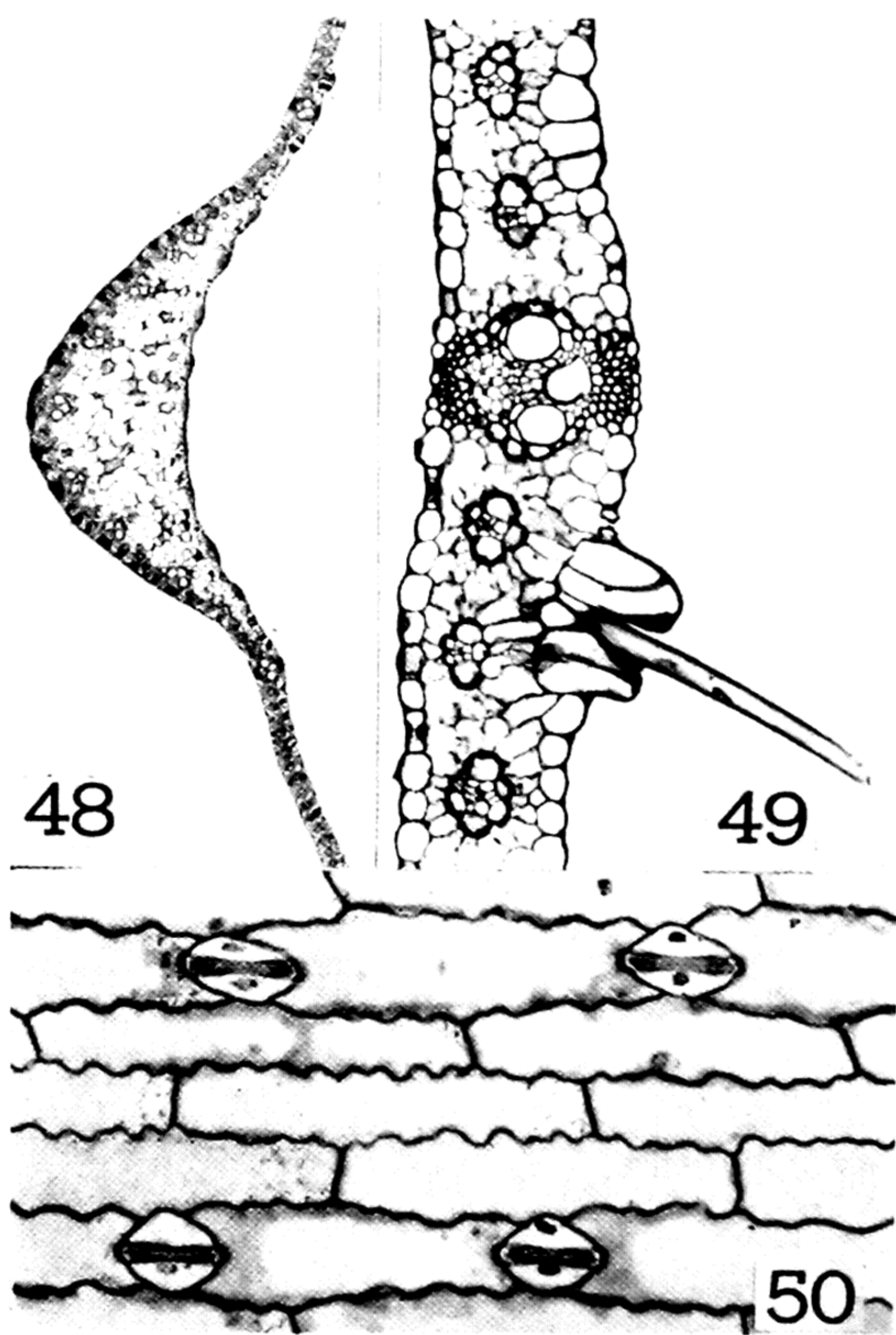


FIG. 48. Transverse section of leaf of sweet corn. 9 $\times$.

FIG. 49. Detail of leaf blade of dent corn. 64 $\times$.

FIG. 50. Surface view of epidermis. 256 $\times$.

lengthwise of the leaf. The guard cells are surrounded by the accessory cells. The ordinary epidermal cells are long and narrow, with undulating side walls.

Inbred lines, hybrids, and varieties of corn exhibit striking differences in the morphology of the epidermis, as well as other leaf characters, such as spacing of vascular bundles, the frequency of cross veins, the amount of bundle sclerenchyma and many other features. Such morphological information has not been systematically and extensively

accumulated, and only limited correlation with agronomic properties is possible at present.

REFERENCES

- ABBE, E. C., and STEIN, O. L. 1954. The growth of the shoot apex in maize embryogeny. *Am. J. Botany* **41**: 285-293.
- BELL, M. E. 1954. The development of the embryo of *Zea* in relation to position on the ear. *Iowa State Coll. J. Sci.* **29**: 133-139.
- BERNSTEIN, L. 1943. Hybrid vigour in corn and the mobilization of endosperm reserves. *Am. J. Botany* **30**: 801-809.
- BONNET, O. T. 1953. Developmental morphology of the vegetative and floral shoots of maize. *Univ. Ill. Agr. Expt. Sta. Bull.* **568**: 5-47.
- ESAU, K. 1943. Ontogeny of the vascular bundle in *Zea Mays*. *Hilgardia* **15**: 327-356.
- FAIRCHILD, R. S. 1953. Comparative development of the embryos of inbred and hybrid maize. *Iowa State Coll. J. Sci.* **27**: 381-405.
- GROSZMANN, A., and SPRAGUE, G. F. 1948. Comparative growth rates in a reciprocal maize cross. I. The kernel and its component parts. *J. Am. Soc. Agron.* **40**: 88-98.
- JOHANSEN, D. A. 1950. "Plant Embryology; Embryogeny of the Spermatophyta," pp. 305. Chronica Botanica Co., Waltham, Mass.
- KIESSELBACH, T. A. 1949. The structure and reproduction of corn. *Nebraska Agr. Expt. Sta. Research Bull.* **161**: 3-96.
- LEDIN, R. B. 1954. The vegetative shoot apex in *Zea Mays*. *Am. J. Botany* **41**: 11-17.
- LENG, E. R. 1951. Time-relationships in tassel development of inbred and hybrid corn. *Agron. J.* **43**: 445-449.
- MAGEE, J. A. 1948. Histological structure of the stem of *Zea Mays* in relation to stiffness of stalk. *Iowa State Coll. J. Sci.* **22**: 257-268.
- MARTIN, J. N., and HERSHEY, A. L. 1935. Ontogeny of the maize plant. The early differentiation of stem and root structures and their morphological relationships. *Iowa State Coll. J. Sci.* **9**: 489-503.
- PICKLUM, W. E. 1953. Histological and cytological changes in the maize embryo during germination. Ph. D. thesis, Iowa State College, Ames, Iowa.
- RANDOLPH, L. F. 1936. Developmental morphology of the caryopsis in maize. *J. Agr. Research* **53**: 881-916.
- SASS, J. E. 1951a. Comparative leaf number in the embryos of some types of maize. *Iowa State Coll. J. Sci.* **25**: 509-512.
- SASS, J. E. 1951b. "Reduced" vascular bundles in maize. *Iowa State Coll. J. Sci.* **26**: 95-98.
- SHARMAN, B. C. 1942. Developmental anatomy of the shoot of *Zea Mays* L. *Ann. Botany (London)* [N. S.] **6**: 245-282.
- TOOLE, E. H. 1924. The transformations and course of development of germinating maize. *Am. J. Botany* **11**: 325-350.

CHAPTER III

Structure and Development of Reproductive Organs

PAUL WEATHERWAX

I. Introduction

When the sixteenth-century herbalist, John Gerarde, came to the task of writing something about "Turkie corne," as the Indian corn plant was currently known in England, he expressed in the following words some of the amazement with which botanists regarded this great American plant when it was first taken to Europe (Gerarde, 1597): "At the top of the stalks grow idle or barren tufts like the common Reede, sometimes of one colour and sometimes of another. Those eares which are fruitful do grow upon the sides of the stalks among the leaves which are thicke and great, so couered with skins or filmes, that a man cannot see them vntill ripenes haue discovered them."

Not only was this separation of the male and female flowers, which set corn off from the other cereals, a source of wonderment at that time; it has been the key to many of the puzzles presented by the plant and has provided the mechanism by which we have manipulated it for our purposes.

II. The Spikelet and Flower

Like all the other cereals, the corn plant bears its flowers in spikelets, the characteristic building blocks of the inflorescences of all grasses, and a recognition of these is the first step toward understanding the reproductive mechanism. The male spikelets are the separate units of which the tassel is made (Fig. 1). They can most easily be recognized before flowering—just as the tassel emerges from the leaves at the top of the plant. The female spikelets are seldom seen as such because they are covered by the husks of the young ear. They can be located by the fact that each of them ordinarily produces one grain.

1. *Male Spikelet*

In what may be regarded as the typical or normal staminate spikelet, a short rachilla bears four bracts, the uppermost two of which (the lemmas) have short flower-bearing branches in their axils. The two low-

est bracts (the glumes) have empty axils as in most grasses. The short branch in the axil of each lemma has, on the side opposite the lemma, a single bract, the palea, and it is terminated by the flower. The immature flower is thus enclosed between the lemma and palea, whose edges overlap. The relationships of the parts of the spikelet are better shown in Fig. 2.

The flower (Fig. 2A) consists of three stamens, two lodicules, and the rudiment of a pistil. The position of the lodicules indicates that they represent a whorl of flower parts outside that formed by the three stamens. They are regarded as the remnants of a perianth which was present in some ancient ancestor. Their function now is to swell within a few minutes at the time of flowering and push back the lemma, allowing the anthers to emerge on their slender, elongating filaments.

2. Female Spikelet

The pistillate spikelet has the same vegetative parts and the same structural plan as the staminate, but its rachilla is so short and its bracts so modified in shape that the homologies between the two spikelets are evident only when sections of the two are examined (Figs. 2A and B). The upper flower of this spikelet consists of a pistil, three rudimentary stamens, and two conspicuous, but apparently functionless lodicules. The entire lower flower of this spikelet is aborted in most kinds of corn, but in a few varieties it quite regularly has a functional pistil, and the spikelet thus produces two grains instead of the usual one (Kempton, 1913; Stewart, 1915; Weatherwax, 1916).

III. The Inflorescences

Another important key to the morphology of the inflorescence, particularly useful in comparing corn with its nearest relatives, is the fact that the spikelets are disposed in pairs on the framework of the inflorescence. This arrangement or some obvious modification of it occurs regularly throughout the grass tribe *Maydeae*, to which corn belongs, and *Andropogoneae*, a heterogeneous group, some members of which are closely related to corn. This grouping of spikelets has also evolved independently in several genera scattered through the other tribes.

1. Terminology

If we substitute *spikelet* for *flower*, the terminology of grass inflorescences is the same as that applied to other flowering plants. This means that when we speak of spike, raceme, or panicle in the grasses, we refer to at least one degree more of complexity than the term ordinarily implies. In the *Maydeae* and *Andropogoneae* the case is still more com-

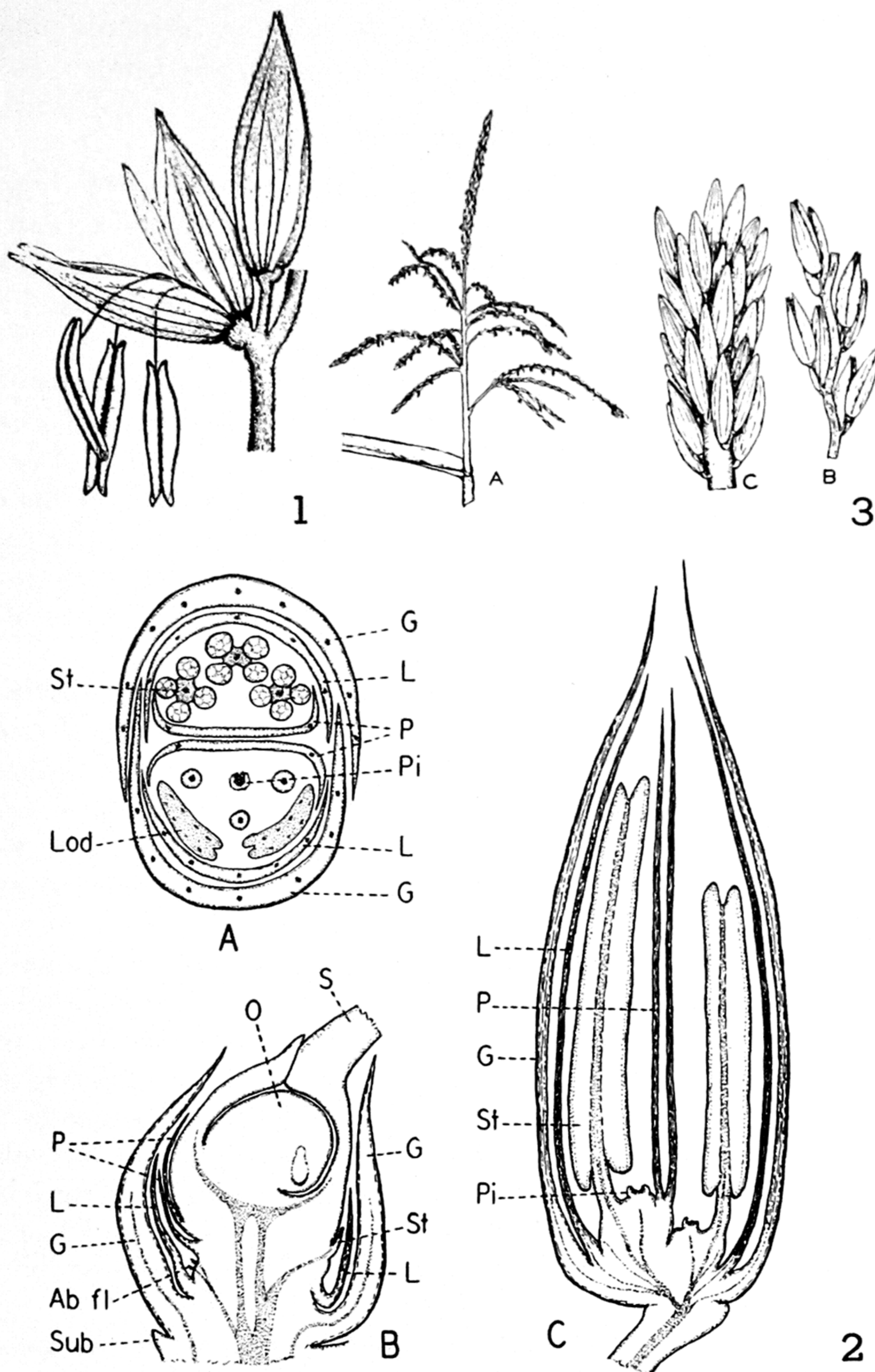


FIG. 1. A pair of staminate spikelets.

FIG. 2. Sections of spikelets. *A*, cross section of a staminate spikelet; *B*, longitudinal section of a pistillate spikelet; *C*, longitudinal section of a staminate spikelet. *Ab fl*, aborted flower; *G*, glume; *L*, lemma; *Lod*, lodicule; *O*, ovule; *P*, palea; *Pi*, aborted pistil of staminate spikelet; *S*, style; *St*, stamen (aborted in pistillate spikelet); *Sub*, bract subtending the pair of pistillate spikelets.

FIG. 3. Staminate tassel (*A*) and arrangement of spikelets on lateral branch (*B*) and on central spike (*C*).

plex because the *pair of spikelets* is the unit of structure, and it is, morphologically, a condensed branch bearing two spikelets.

2. Male Inflorescence

In this terminology the male inflorescence is a broadly expanded panicle of pairs of spikelets. Its framework consists of a central axis and a few to many spreading branches. In rare instances it may consist of only the single spike. In large inflorescences the lateral branches may themselves branch repeatedly (Fig. 3).

On the terminal portions of these lateral branches the pairs of spikelets are arranged in two rows along the dorsal side. The result is a dorsiventral branch bearing four rows of spikelets, one member of each pair being sessile and the other pedicellate. On the upper part of the central axis of the tassel, above the uppermost lateral branches, the pairs are arranged in two, or usually more than two, rows, so that the structure bears four, or, in even numbers, usually more than four rows of spikelets.

All these spikelet-bearing branches of the tassel are usually designated as *spikes*, and this term is probably as good as any if we remember that it has a special meaning here. Since half of the spikelets are pedicelled, the branch has some of the character of a raceme; and, since the pairs of spikelets represent reduced branches, it is obvious that the whole structure has a significant complexity which is not covered by the ordinary definition of the word *spike*.

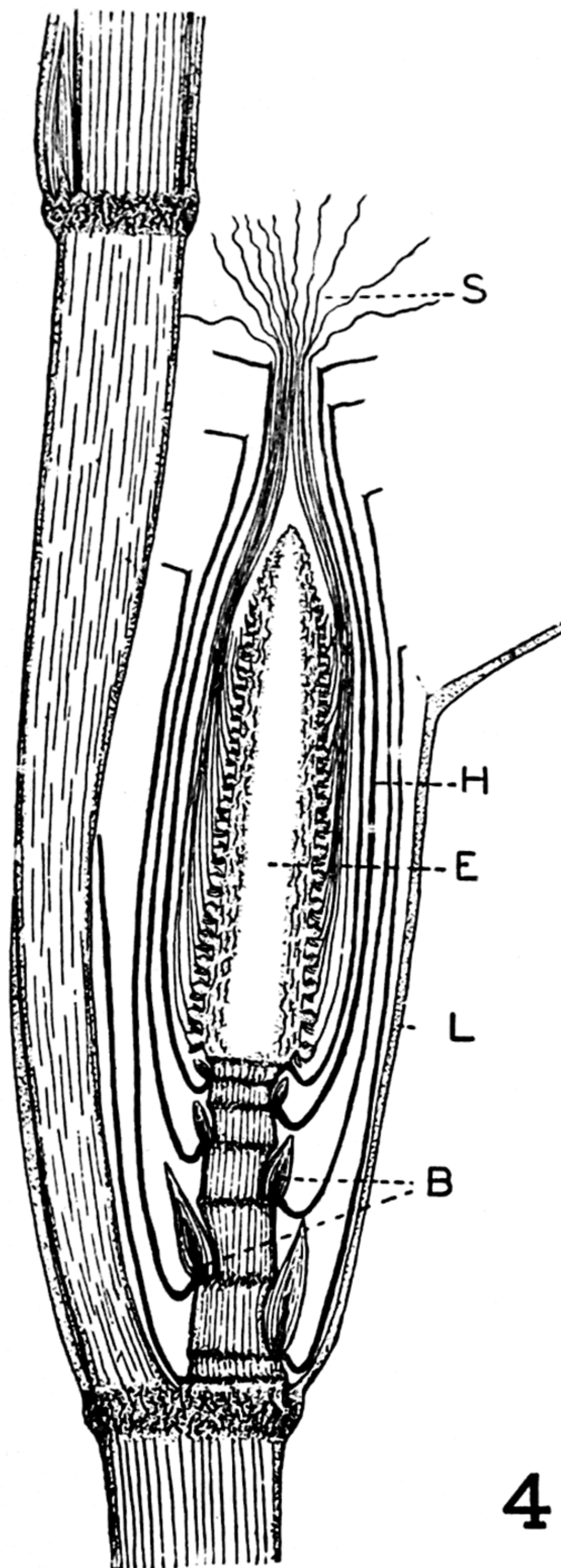
Regularly in some varieties of corn, and occasionally in almost any variety, the staminate spikelets may seem to be arranged in whorls or other groups of more than two. On close inspection, however, most of these groups can be resolved into close aggregations of pairs which have resulted from the failure of internodes of the axis to elongate during development. This is an expression of a tendency widely prevalent in the vegetative and floral morphology of the *Gramineae*. It may be that when a better analysis of it is available, this peculiarity will go a long way toward explaining some complicated structures such as the ear of corn.

Another interesting point which is well known, but in the consideration of which theory and practice are often far apart, should be noted here. The peduncle of the tassel elongates by means of a meristem located at its lower end, at the bottom of the sheath of the uppermost leaf of the plant. This method of growth, which thrusts the tassel upward beyond the leaves at flowering time, is a part of the vegetative pattern of the grass family in general. It is also of great practical importance because it maintains a physically weak place in the peduncle and makes it possible to remove the tassel by simply pulling it upward.

If a corn plant were constructed on the same pattern as most dicotyledonous plants, the task of detasseling corn as a breeding technique would be increased many fold.

3. Ear Branch

The lateral branch which bears the female inflorescence and later the ear of the corn plant has resulted from the phylogenetic shortening of a structure similar to the main stem (Fig. 4). The internodes of this



4

FIG. 4. Diagram of longitudinal section of ear branch attached to main stem. *B*, buds in axils of husks; *E*, ear; *H*, husk of ear; *L*, leaf subtending the ear branch; *S*, styles.

have become so short that the overlapping sheaths of its leaves cover the terminal inflorescence, forming the well-known husks of the ear. These leaves show various degrees of modification in structure. Their blades may be well developed, variously reduced, or entirely lacking. The widened sheaths become progressively thinner and softer in texture from the outer husks inward. The potential branches in the axils of these husks may, in different varieties and under different conditions, range all the way from meristematic rudiments to fully developed ear-bearing branches (Weatherwax, 1923). In some primitive varieties grown by the Indians of Mexico, Central America, and the Andes, it is not uncommon to find these axillary branches producing secondary ears large enough to be worth harvesting (Fig. 5). In most varieties they may, under favorable conditions, produce small ears with a few grains.

4. *Pistillate Inflorescence*

The pistillate inflorescence and the ear developing from it have been the subject of much study and controversy, and many theories have been proposed to explain them (Weatherwax, 1935, pp. 40–52; Mangelsdorf and Reeves, 1939, pp. 54–61). The inflorescence consists of a thick axis—the “cob” of the ear—on which the pairs of spikelets are arranged in longitudinal rows. The primary branch of this axis, which bears a pair of spikelets, is so short that the spikelets, and later the grains, seem to be attached directly to the cob. It is possible, however, to demonstrate the true structure by removing pairs of grains still attached to the stalk which bears them (Figs. 6, 7). Since a row of pairs of spikelets bears 2 rows of grains, it follows that the ear usually has an *even* number of rows of grains.

Individual ears of corn may have from 4, in even numbers, to 30 or more rows of grains. This means that they have from 2 to 15 or more rows of pairs of spikelets. The number of rows on an ear is determined partly by heredity, but, especially in varieties with high numbers, the number may be affected by environment. Different numbers of rows may sometimes be found in two or more ears on a single plant.

A 4-rowed ear, having 2 rows of pairs of spikelets, conforms with the 2-ranked vegetative pattern of grasses, a pattern which also occurs regularly, in one way or another, in the inflorescences of grasses. But such ears occur very infrequently. The typical ear, with 8 or more rows of grains, has, therefore, been regarded as something of an anomaly in the grass family, and, consequently, a thing requiring some sort of explanation.

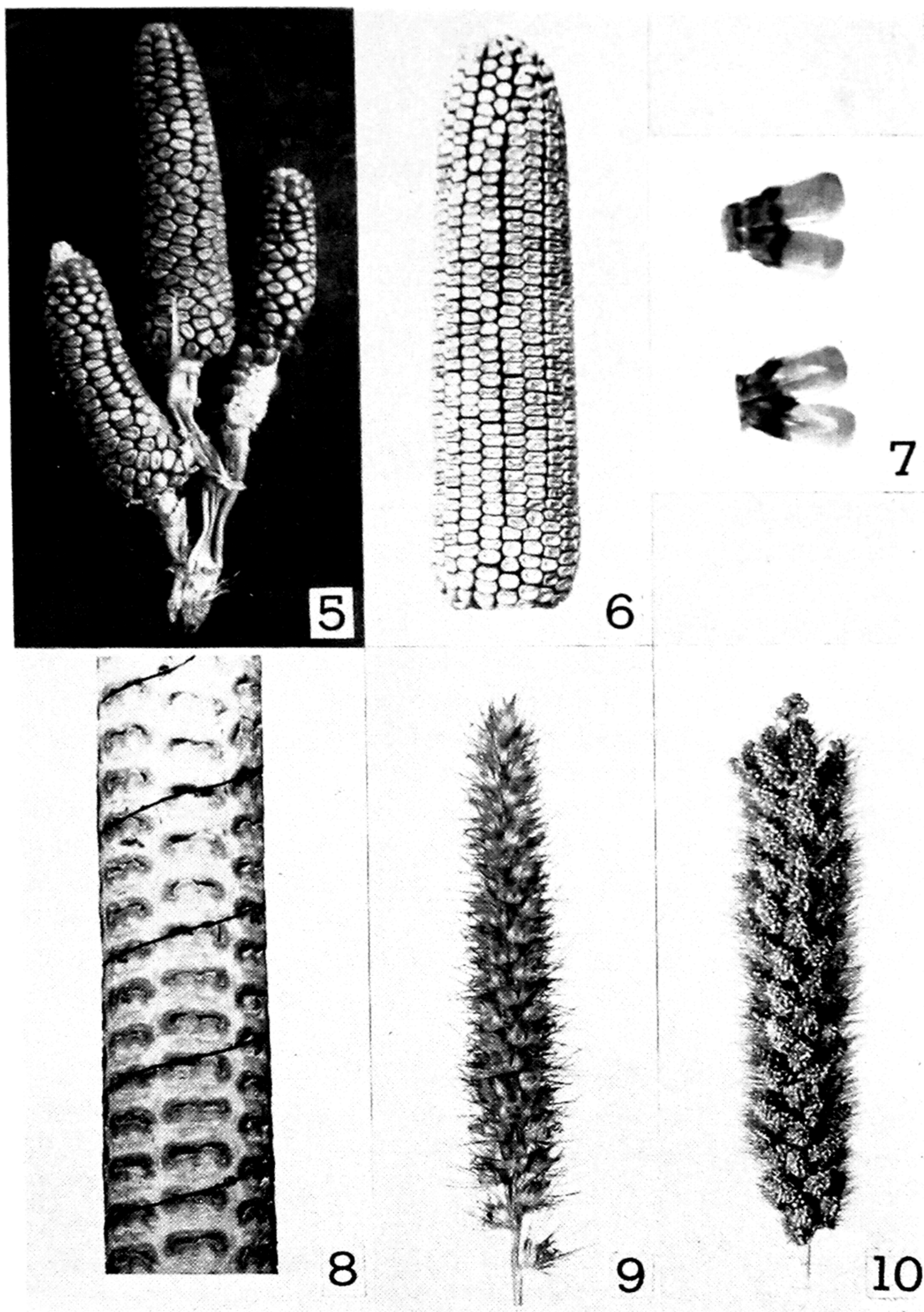


FIG. 5. Ear branch of a tropical variety, showing well-developed secondary ears in axils of husks.

FIG. 6. A well-developed ear of a commercial variety of dent corn.

FIG. 7. Pairs of grains removed from an ear like that shown in Fig. 6.

FIG. 8. Cob with bracts shaved off to show spiral arrangement of pairs of spikelets.

FIG. 9. Inflorescence of *Cenchrus pilosa*, showing spiral arrangement of burs, which are fascicles of spikelets.

FIG. 10. Inflorescence of *Setaria italica*, showing spiral arrangement of fascicles of spikelets.

a. Interpretation of the Ear. One of the earliest attempts to explain the structure of the ear of corn from the evolutionary standpoint assumed that it arose from a teratological fusion of simpler spikes like those forming the lateral branches of the male tassel (Hackel, 1887, p. 20). This seemingly plausible explanation was apparently supported by the way in which these branches are crowded closely together, side by side, in the developing tassel. Occasionally branched ears were thought to have resulted from the "disruption" of this compound structure.

It has long been noted, however, that the central spike of the tassel also has several rows of pairs of spikelets and is as much in need of explanation as its homologue, the ear itself (Kellerman, 1895; Montgomery, 1906). Aside from the fact that we have no clear picture as to how such a phylogenetic fusion of anatomical parts could have taken place, there was the further question of how lateral spikes, each contributing 4 rows of spikelets, could have been added together to form an ear with 6, 10, 14, or 18 rows of grains—that is, an ear with rows not in multiples of 4. This idea that the ear is a product of phylogenetic fusion is a hard one to keep down, however, and, in spite of overwhelming evidence to the contrary, it is still widely entertained by many who have made little firsthand study of the plant.

Another approach to the problem showed that when the chaff is removed from the cob of a mature ear, as when it is to be used for making a corncob pipe, the branches which bear pairs of spikelets are found to fall in a series of spirals (Fig. 8). The number of these spirals is correlated with the number of rows of grains, and the pitch of the spiral determines the shape of the cross section of the grain (Weatherwax, 1935, p. 48).

Since each pair of spikelets is located in the axil of a hypothetical leaf, the rudiment of which is usually visible, the problem becomes one of phyllotaxy, and the thing to be explained is only the change from the distichous pattern of most grass inflorescences to the spiral one of the corn inflorescence. It was only when attention was shifted from the longitudinal rows of grains to this spiral arrangement of the pairs of spikelets that we began to make substantial progress toward an understanding of the morphology of the ear of corn.

The ontogeny of this structure as a phenomenon of spiral phyllotaxy was clearly described more than 60 years ago (Schumann, 1890), but its bearing on the problem of phylogeny was overlooked in the early attempts to explain the origin of the ear of corn.

A re-examination of the inflorescences of some other genera of grasses—*Pennisetum*, *Setaria*, *Cenchrus*, *Tragus*, and *Antheophora*, for

example—shows that the spiral arrangement of fascicles of spikelets is of wide occurrence and that the ear of corn is not, in this respect, the unique and mysterious structure that it was once supposed to be (Figs. 9, 10; Weatherwax, 1935, pp. 45, 46).

b. Structure of the Cob. The axis of the ear, that is, the corncob, varies in structure from one kind of corn to another, but the significant features of all these can be reduced to a single pattern. Its vascular tissue, accompanied by a complex system of sclerenchyma and lignified parenchyma, forms a hollow cylinder, the middle of which is filled with a soft parenchyma without vascularization. The full development of these hard mechanical tissues seems to depend on some hormone stimulus following fertilization and accompanying the development of the grains.

By retting away the parenchyma chemically or through the action of bacteria, it has been shown that the vascular tissue really consists of two hollow cylinders, one inside the other (Laubengayer, 1948; Reeves, 1946). The full analysis of this pattern promises to throw much light on the phylogeny of the ear as well as on some broader problems of plant anatomy.

IV. Development of Flower and Inflorescence

The development of the inflorescence begins when the low, hemispherical apical meristem which has been producing vegetative parts abruptly changes to a slender, conical one and begins to form the initials of spikelet-bearing branches. At first the young male and female inflorescences look very much alike, but the lowest primordia of the one elongate and begin the formation of the lateral branches of the terminal tassel. In the young ear these branches simply fail to develop.

In both inflorescences the short branches, each of which is to produce a pair of spikelets, arise as smooth, rounded protuberances, and a division of each of these into two lobes, one a little taller than the other, gives rise to the initials of the spikelets. The taller primordium produces the pedicelled spikelet of the male inflorescence (Bonnet, 1940, 1948). In the mature ear a slight asymmetry in the pair of grains reflects this morphological difference between the two spikelets.

Although the formation of these spikelet primordia proceeds in an acropetal direction on all axes of the inflorescences, the spikelets themselves do not necessarily reach maturity in that order. The first staminate spikelets to mature are located a short distance below the tip of the central spike of the tassel, and these are soon followed by spikelets near the tips of the lateral branches. As the young ear develops, the

spikelets located a short distance above the base are the most advanced, and maturity proceeds upward and downward from that level.

1. The Spikelets

In early stages of development the male and female spikelets are almost exactly alike. The first differentiation to appear is the formation of the lower glume, and this is soon followed by the appearance of the upper one. The two lemmas next arise almost simultaneously with the

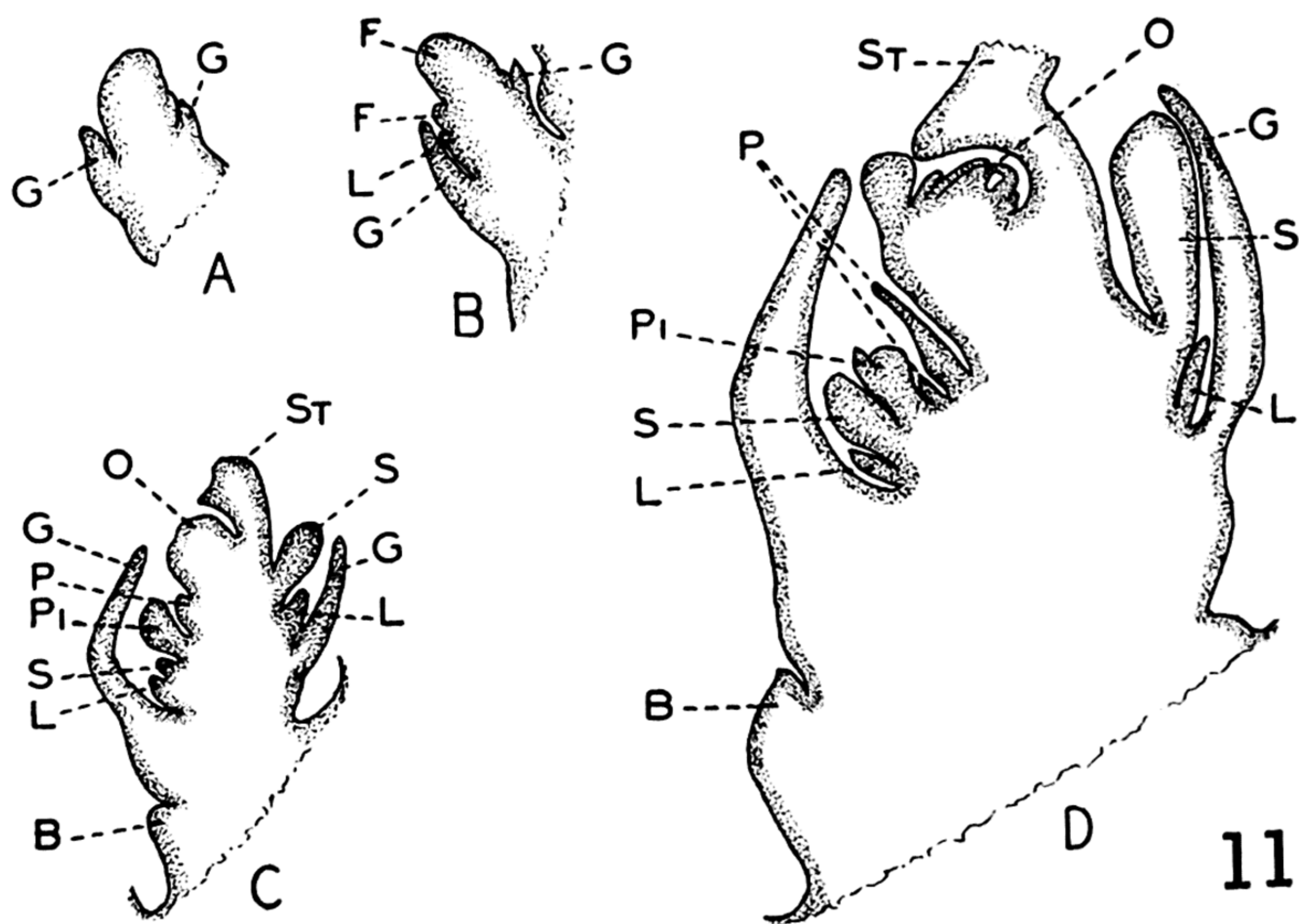


FIG. 11. Development of a pistillate spikelet. *B*, bract subtending the pair of spikelets; *F*, flower primordium; *G*, glume; *L*, lemma; *O*, ovule; *P*, palea; *Pi*, pistil; *S*, stamen; *St*, style.

differentiation of the three stamens of the upper flower of the spikelet. From the lower side of the remaining undifferentiated part of the spikelet now arises the primordium of the lower flower, and the two paleas appear last (Fig. 11). The older floret seems to be terminal and the younger one lateral on the rachilla, but there are morphological questions here which merit further investigation (Weatherwax, 1917, p. 485; Kiesselbach, 1949, pp. 37-42).

2. The Flowers

In the development of the flower from its primordium, the stamen initials appear slightly in advance of the lodicules, and the remaining meristem becomes the pistil. As the stamens and pistil begin to take on

recognizable form, sexual differentiation begins, and with it comes a divergence in the outward appearance of the male and female spikelets which ultimately leads to such a difference between the two that their homologies have often been overlooked.

a. Staminate Flower. In both flowers of the male spikelet the stamens and lodicules develop fully and function as in other grasses; but the development of the pistils is early arrested, and at flowering time they are represented by rudiments so inconspicuous that they were entirely overlooked in the early taxonomic descriptions of the genus (Weatherwax, 1916, p. 130).

The lodicules make their appearance as small protuberances and develop into thick, short bodies whose truncated tops are indented by contact with the lower ends of the anthers during development. They are well supplied with vascular tissue, and some abrupt physiological change at anthesis causes a movement of water into them so that they swell to three or four times their former size and wedge the lemma and palea apart, allowing the stamens to emerge.

The development of the stamen is much the same as in other plants. In each loculus of the anther a long core of pollen mother cells is surrounded by three layers of tapetal cells, which disappear by flowering time, leaving only the epidermis as the outer wall of the loculus (Fig. 12). For a short distance at the distal end of the anther this epidermal layer is reinforced internally by a layer of mechanical cells with the characteristic annular thickenings on their walls. By action of these cells a pore is formed for each pair of loculi when the time comes for the release of the pollen (Figs. 1, 12). It is only for this short distance at the tip of the anther that the adjacent loculi coalesce to form the characteristic anther "cells." The filament of the stamen is short and thick until anthesis, when, within a few minutes, it increases enormously in length, carrying the anther far beyond the covering of bracts (Weatherwax, 1917, p. 486; Kiesselbach, 1949, pp. 41-48).

Meiosis and the events immediately following it do not present any unusual features except that the maturation process goes one step farther than in most plants, and the two long, crescent-shaped sperms are formed before the pollen grain leaves the anther (Guignard, 1901; Weatherwax, 1919; Miller, 1919). The mature pollen grain (Fig. 13) is almost spherical. The exine is minutely roughened, and there is a prominent germ pore, surrounded by a thickened ring and loosely closed with a plug of material similar to the rest of the wall.

The abortive pistil of the male flower varies a great deal in development in widely different varieties and under different environmental conditions, but it is remarkably uniform in the ordinary highly im-

proved varieties (Fig. 14). It develops as in the female flower—to be described later—up to the point where the ovary wall should begin to form and then begins to disorganize internally. The epidermis is the

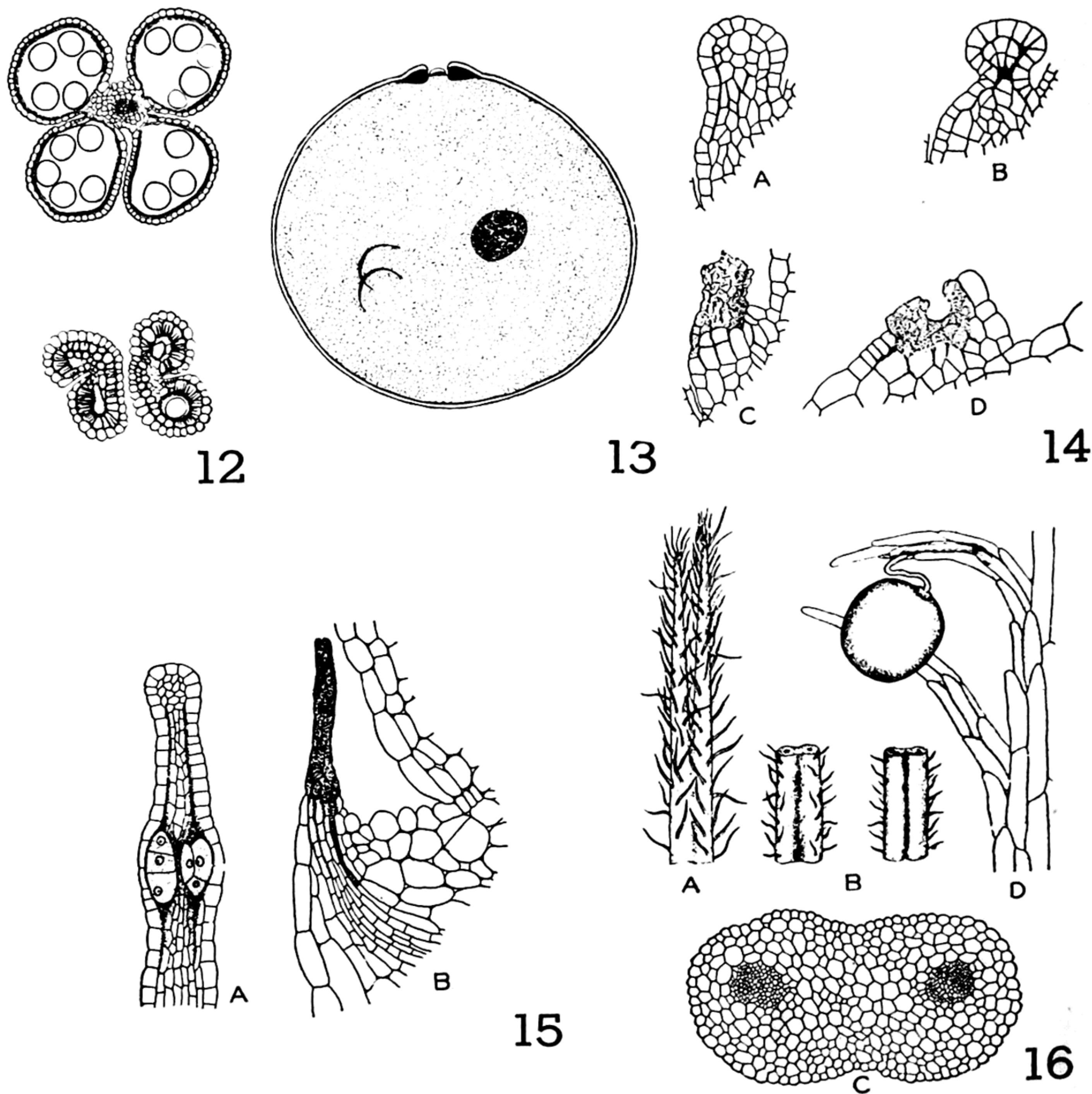


FIG. 12. Cross section of an anther near the middle and near the tip.

FIG. 13. Section of a mature pollen grain.

FIG. 14. Steps in the abortion of the pistil of a staminate flower.

FIG. 15. Steps in the abortion of the stamen of a pistillate flower.

FIG. 16. Tip (A), intermediate segments (B), and cross section (C) of style; D, pollen grain germinating on style.

last part to go, and a small, cuplike remnant of it is all that is left of the pistil at the time of flowering (Weatherwax, 1917, p. 487).

b. Pistillate Flower. Although the female spikelet has at first exactly the same pattern as its male counterpart, the only floral structure which

ordinarily persists to functional maturity is the pistil of the upper flower. The bracts remain short. The lower portions of the glumes become thick and corneous and often show characteristic sculpturing on their surfaces, but they taper out to thin, hyaline membranes at their tips. These, with the lemmas and paleas, are usually left to form the chaffy covering of the cob when the grains are removed.

The lodicules of both flowers of this spikelet grow for a time, but their development is soon arrested. They do not disorganize after the manner of other suppressed organs but simply cease to grow and are overtaken by the growth of the surrounding tissues. At anthesis those of the upper flower have almost disappeared in this way, but those of the lower flower are relatively conspicuous even in those instances in which the flower has a functional pistil. They do not seem to be of any functional significance in either flower.

Disorganization seems to begin simultaneously in all the other suppressed organs of the pistillate spikelet; and the stamens and pistil of the younger, lower flower, being caught by the process at an earlier stage, show less development than the stamens of the upper flower. The fate of the pistil of the lower flower is much as in that of the staminate flower. The stamens usually develop to about the point which the anther and filament should differentiate, and then disorganization begins internally (Weatherwax, 1917, p. 492).

Before the arresting influence becomes effective, the stamens of the upper flower have usually made sufficient development that the tapetum and a few pollen mother cells are differentiated (Fig. 15). Disorganization begins in the tapetal region and extends to the other tissues, but the epidermis often remains intact (Weatherwax, 1917, pp. 492-494). At anthesis these stamens may sometimes be seen as inconspicuous, disorganized appendages at the base of the pistil, but occasionally they are larger and show externally the miniature form of normal stamens. In many instances they are large enough to be seen externally as they protrude between the grains of a mature ear.

After the appearance of the stamens of the functional pistillate flower, the small, rounded protuberance which remains becomes the primordium of the pistil. Near the base of this a ring of tissue begins to grow upward to form the ovary wall. The sides of this converge a little to one side of the top of the structure, but they never fuse. The stylar canal which is thus left as an opening into the ovarian cavity has no function and is to be regarded as only an incidental result of the method of growth (Fig. 11). Meanwhile, a projection of the ovary wall, on the side toward the lemma, is soon recognizable as the beginning of the style, commonly known as the corn "silk" (Weatherwax, 1917, pp. 489-491; Miller, 1919, pp. 259-261; Kiesselbach, 1949, pp. 53-56).

From the time at which it can first be recognized, the style is divided at the tip, and this division continues to maturity as two shallow grooves running full length of the structure. This sort of style, which is peculiar to corn and teosinte, seems to be a compound organ, the equivalent of the two styles of most other grasses. It grows rapidly by means of a meristematic region near its base and may finally reach a length of a foot or more (Fig. 16).

Each of the stigmatic hairs, which are scattered the full length of the style, even on the parts which are covered by the husks of the ear,

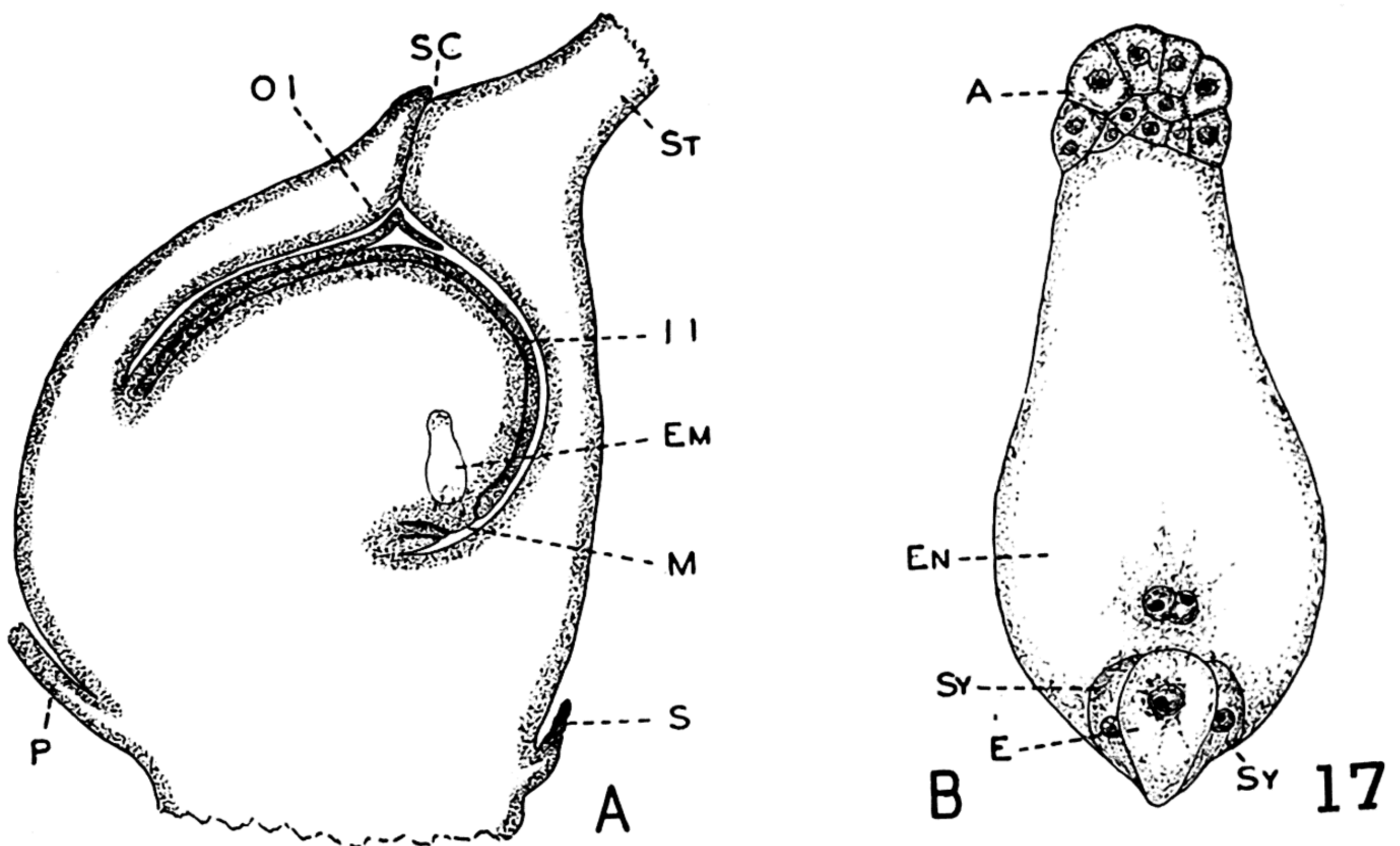


FIG. 17. Longitudinal section of mature ovary (A) and embryo sac (B). A, antipodal cells; E, egg; Em, embryo sac; En, endosperm cell; II, inner integument; M, micropyle; OI, outer integument; P, palea; S, rudimentary stamen; SC, stylar canal; St, style; Sy, synergids.

originates from a single cell. When fully developed it consists of four rows of cells loosely fitted together, with an intercellular canal extending lengthwise through it (Weatherwax, 1917, p. 491).

As the pistil develops, the primordium of the single ovule grows upward in the cavity of the ovary. The integuments arise around its base as two separate collars of tissue. The integuments and nucellus grow rapidly on the side which is oriented toward the palea, and very little on the other side, so that, by the time of fertilization, the ovule has become completely inverted (Figs. 2, 11, 17). The edge of the outer integument usually becomes wedged into the stylar canal so that it does not grow entirely over the ovule and takes no part in the formation of the micropyle (Weatherwax, 1917, p. 491; Miller, 1919, p. 259).

V. Gametophytes and Fertilization

At about the time of the first appearance of the integuments of the ovule, the megaspore mother cell becomes differentiated. Meiosis is followed by the disorganization of three of the megaspores, and the remaining one proceeds to form the gametophyte in much the same manner as in other grasses. When the embryo sac is first organized, it consists of the usual seven cells, but the three antipodal cells now begin a process of division which results in a mass of 25 or more vegetative gametophytic cells. The two polar nuclei come together near the egg but do not fuse or make further development until fertilization occurs (Guignard, 1901; Weatherwax, 1919; Miller, 1919).

1. Pollination

When the stamen emerges and the anther opens, the pollen is not all released at once but is spilled out a little at a time as the anther dangles at the end of its filament. Any movement of the plant helps to shake out the pollen, and it is usually all discharged within a few hours at most. The wind is the principal agency accomplishing this, and the pollen is also carried to the stigma by the wind. Honey bees, and occasionally other insects, collect large quantities of the pollen, but they apparently have no occasion to visit the pistillate parts of the plant, and they are probably not to be regarded as agencies of pollination.

Wind pollination is wasteful here as usual. Counts and computations made on a commercial dent corn indicate that an individual plant produces probably 50,000 pollen grains for each one that becomes effective in producing a grain of corn. In some tropical varieties with large tassels and small ears the ratio is probably much higher.

There is much variation in the relative times of maturity of the male and female inflorescences of individual plants. A degree of protandry is the rule, but varieties are known in which protogyny prevails. There is usually enough overlapping of the release of pollen and the receptivity of the silks to make some self-pollination possible. In some varieties, however, there is such a wide difference in time of maturity of the two inflorescences that there is no possibility of self-pollination. Experiments show that, under ordinary field conditions, seldom as many as 10 per cent of the grains of an ear result from self-pollination.

2. Pollen Tube

When the pollen grains fall on the moist surfaces of the style or the stigma hairs they adhere there, and the moisture promotes germina-

tion. The pollen tube may penetrate the body of the style directly, but it usually enters by way of one of the stigmatic hairs (Fig. 16). Once inside the tissues of the style it follows one of the strands of vascular tissue toward the ovary (Miller, 1919, pp. 261–262; Kiesselbach, 1949, pp. 63–67).

This step in the reproductive process, when the slender, unprotected pollen tube is fully exposed to the air for a time, is a critical one, as is effectively shown by the disastrous effects of high temperatures or drying winds at the time of pollination.

In its long course from the place where the pollen grain germinates to the ovule, only a short segment of the pollen tube is alive at any one time. In longitudinal sections of the style this living part appears as a short, thick body of dense cytoplasm in which the tube nucleus and the two sperms can be seen only with difficulty.

After the pollen tube has passed any particular level in the style, the tissues of the latter close around the pathway of the tube so completely that its course can scarcely be detected. At the top of the ovary the pollen tube leaves the base of the style, enters the ovarian cavity, and apparently follows the inner surface of the ovary wall until it comes to the micropyle.

Varieties of corn differ so much, and the process is surrounded with so many other variables, such as temperature and humidity, that it is difficult to make any general statement about the time which elapses between pollination and fertilization. The distance from the pollen grain to the ovule in some varieties is less than an inch, and at the other extreme it may be well above 2 feet. It is not surprising, therefore, to find much variety in the statements on this point. In one small-eared variety of sweet corn which has been observed closely while growing under good conditions of temperature and humidity, the pollen grains had germinated and the tubes were entering the hairs of the stigma one hour after pollination. At the end of 2 hours the tubes were well established in the styles, and the peak frequency of fertilization was found at 25 hours after pollination (Weatherwax, 1919, pp. 77–79).

3. Fertilization

The details of fertilization in corn were first published by Guignard in 1901. The union of one of the sperms with the egg was a readily acceptable fact at that time, but the fusion of the nucleus of the second sperm with the two nuclei of the endosperm cell was at first received with skepticism by many, although it provided a perfect explanation of the phenomenon of *xenia* in corn. This report by Guignard has, however, been fully substantiated by subsequent cytological investigations

of the fertilization process and further corroborated by extensive genetic studies (Weatherwax, 1919; Miller, 1919).

VI. Other Maydeae

Of the seven or eight genera comprising the grass tribe *Maydeae*, to which corn belongs, only two others, *Euchlaena* and *Tripsacum*, have any significant bearing on problems in which corn is involved. Representatives of these genera differ from one another and from corn in many points of external appearance, but they all conform with one general structural pattern.

Aside from the taxonomic descriptions, these genera and the *Maydeae* of the Eastern Hemisphere have been described many times in relation to the problem of the origin of corn. For a full discussion of their structure and relationships and a criticism of the various theories see: Mangelsdorf and Reeves, 1939; Weatherwax, 1918, 1926, 1935, 1950.

1. *Euchlaena*

Euchlaena is a wild plant widely distributed as a weed in cultivated fields and wastelands from north central Mexico to Honduras. The species most often encountered, *E. mexicana* Schrad., is commonly known as *teosinte*. A perennial form, *E. perennis* Hitchc., has been found in a single locality in Mexico (Hitchcock, 1922), but the original colony of it has been destroyed, and it is preserved only in experimental cultures.

In external appearance a teosinte plant, with its terminal tassels and conspicuous lateral "ears" with long silks at flowering time, might well be mistaken for only a peculiar variety of corn (Fig. 18). This has led many to the plausible but entirely erroneous conclusion that it is unmistakably wild corn. Some anthropologists and many popular writers have jumped to conclusions on this point, and at least two experiments have been reported in which, it is alleged, teosinte was changed into corn by a simple process of selection. In both of these experiments, however, it is evident that the plants on which they were based were hybrids of teosinte and corn (Weatherwax, 1925).

Since corn and teosinte hybridize freely where they flower at the same time, and backcrossing of the hybrids with either parent readily occurs, it is difficult to picture uncontaminated teosinte. There are varieties, however, which are sufficiently uniform genetically that it may be assumed that they represent the species fairly well.

a. Inflorescences. The male spikelets and the tassel in which they are borne are so much like those of corn that no further description is necessary except for one characteristic. The teosinte tassel has nothing

corresponding exactly to the terminal spike of the corn tassel; that is, it has no axis on which pairs of spikelets are borne in more than two rows. It may be that a terminal spike in teosinte simply bears only two rows, but there is some indication that there is no true terminal spike.



18

FIG. 18. Habit of teosinte.

The lateral "ear" branch is a deceptive structure (Figs. 18, 19). Seen externally it often resembles a small ear of corn. When dissected out it proves to be an indeterminately branched structure, each ramification of which is terminated by a short spike enclosed in a spathe (Fig.

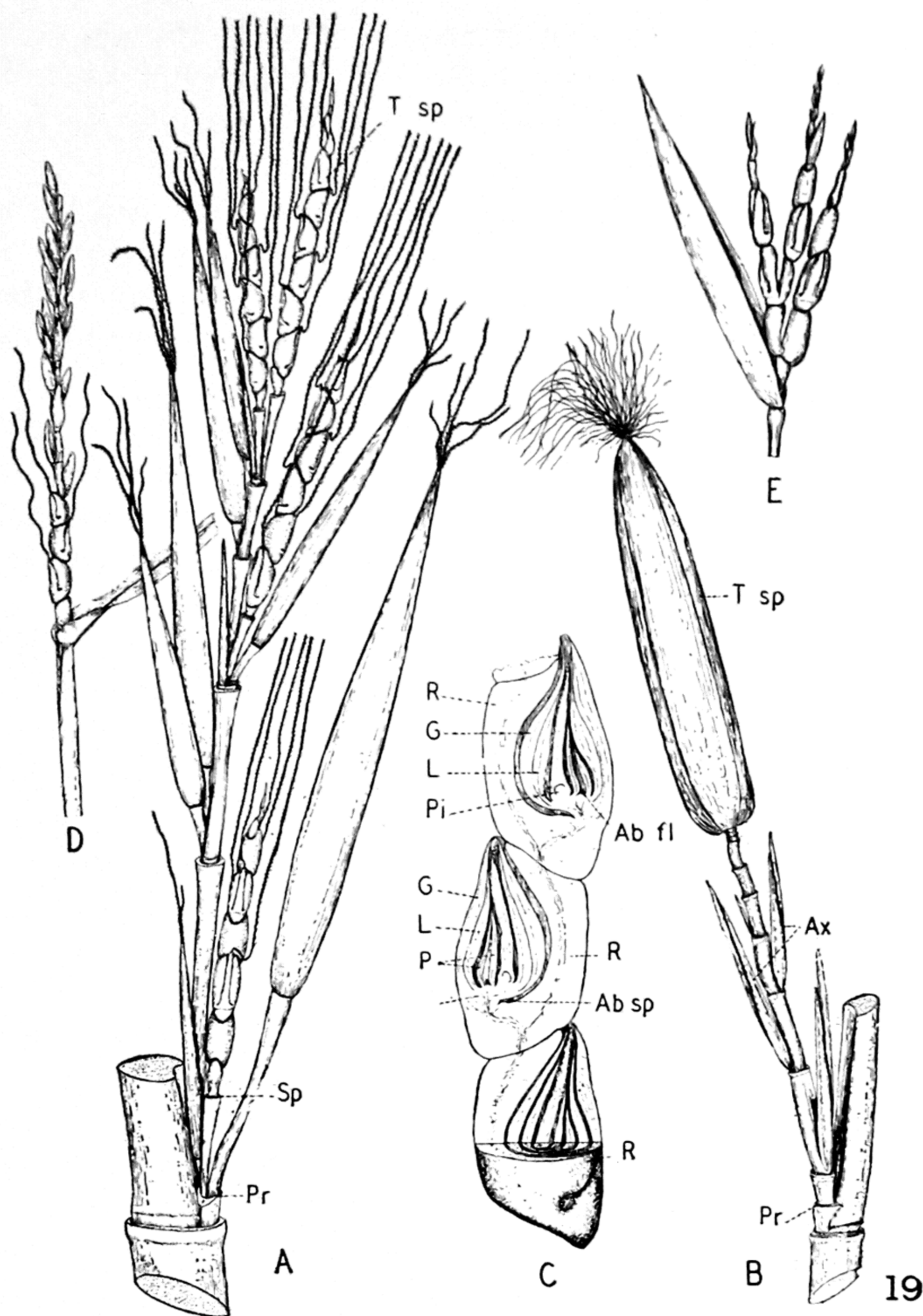


FIG. 19. Comparison of the pistillate branch of teosinte (A) with that of corn (B). C, pistillate spikelets of teosinte; D, mixed inflorescence of teosinte; E, branched pistillate spike of teosinte. *Ab fl*, aborted flower of pistillate spikelet; *Ax*, buds in axils of husks of ear of corn; *G*, glume; *L*, lemma; *P*, palea; *Pi*, pistil; *Pr*, prophyll; *R*, rachis; *Sp*, base of spathe which has been cut away; *T sp*, terminal spike of the inflorescence.

19A). These spikes are the homologues of ears of corn, and the comparison is best seen by recalling that in some tropical varieties of corn there is a tendency for the buds in the axils of the husks to develop into ears (Figs. 5 and 19B).

Each of these ultimate spikes consists of two rows of pistillate spikelets borne alternately in alveoli in a thick rachis. These spikelets seem

to occur singly, but by the side of each of them there is a microscopic rudiment of the other member of the pair (Fig. 19C) (Weatherwax, 1918, pp. 321–322). Rarely this spikelet may develop to functional maturity.

In development and mature structure the pistillate spikelet is essentially like that of corn, although some of the parts have a different superficial appearance. It is so oriented in its attachment to the rachis that its indurated lower glume forms a tight cover over the cavity in which the spikelet is imbedded.

As far as they are known, the morphological details of pollination, gametophyte development, and fertilization are essentially the same as in corn. The large number of inflorescences on a plant and the longer period of flowering do, however, bring about a higher percentage of self-pollination than is found in corn.

b. The Fruit. At maturity the rachis breaks into pieces, each bearing one spikelet with its enclosed fruit. The apparent arrangement of these “seeds” in a single row has led to some loose descriptive terminology and much misunderstanding about their relations to their homologues in corn. This structure can be correctly interpreted only as a rachis bearing pairs of spikelets alternately arranged in two rows, with one member of each pair aborted.

2. *Tripsacum*

The seven recognized species of *Tripsacum* have a combined range from the southeastern quarter of the United States southward to Paraguay (Cutler and Anderson, 1941). In spite of the many differences which serve to distinguish the species from one another, their reproductive structures are morphologically much alike.

a. The Inflorescence. The inflorescence may consist of a single spike, a fascicle of spikes, or a loose, open panicle, with pairs of staminate spikelets in the upper part of each branch, and, below these, what would seem externally to be single pistillate spikelets located in deep cavities in the rachis much as in teosinte (Fig. 20). By the side of each of these, however, there is again the microscopic rudiment of a lost member, completing the pattern of paired spikelets (Weatherwax, 1918, p. 325). In rare instances both members of the pair develop (Fig. 20B).

In the essentials of their structure the male and female spikelets are like those of corn and teosinte. A few clons of *T. dactyloides* have pistillate spikelets in which both flowers are functional and two fruits are produced, this being comparable with what happens in some varieties of corn.

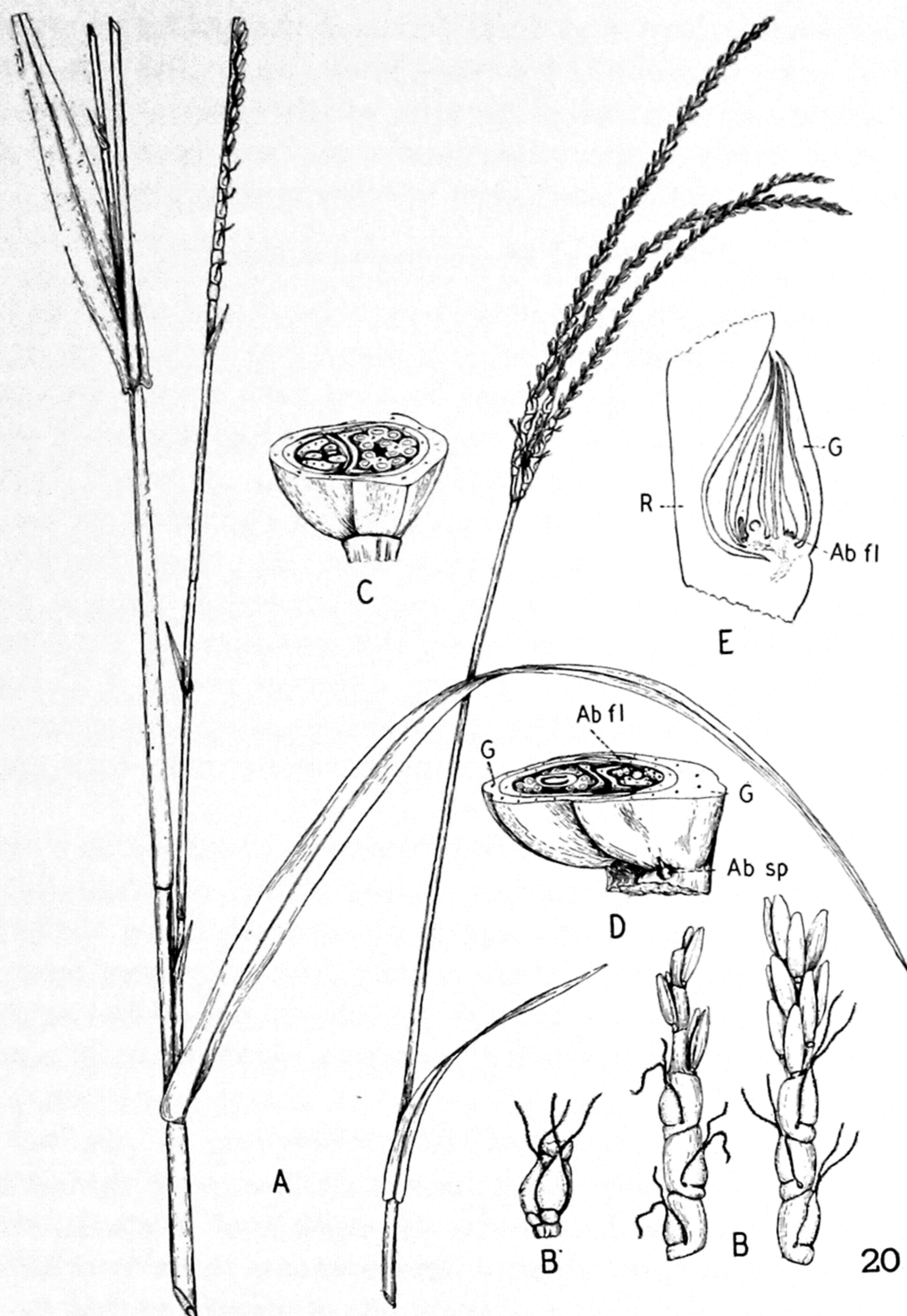


FIG. 20. Inflorescences of *Tripsacum dactyloides*. *A*, terminal and axillary inflorescences; *B*, male and female spikelets; *C*, cross section of staminate spikelet; *D*, cross section of pistillate spikelet; *E*, longitudinal section of pistillate spikelet. *Ab fl*, aborted flower of pistillate spikelet; *Ab sp*, aborted pistillate spikelet; *G*, glume; *R*, rachis.

b. Embryology. Fertilization and the early stages of embryo development in *T. dactyloides*, which has been studied more than any other species in the genus, show many irregularities. In some instances 50 per cent or more of the seeds have two or more embryos, and certain forms of apomixis seem to be common. There are also many irregulari-

ties in the development and final form of the pollen (Farquharson, 1953, 1954, and unpublished data). These anomalies are associated with a complex cytological picture in which various degrees of polyploidy occur. Such further observations as have been made indicate that similar irregularities may occur in other species also.

VII. Floral Abnormalities in Corn

So great has been the part played by agricultural practices in shaping the present-day aspect of the corn plant that such terms as *typical* or *normal*, or their opposites, must be used with some reservations in speaking of it. The plant has evidently shown a high degree of plasticity for a long time, and new characteristics which appeared during the prehistoric period were retained or discarded according to the whims or superstitions of the primitive agriculturist. Its present form is, therefore, to a large extent the result of man's choice. If natural processes had been allowed to have their way, the evolution of the corn plant would doubtless have traveled a very different route, if it had been able to survive at all. As a matter of conjecture, it may be suggested that teosinte is a plant which, after parting company with corn along the evolutionary way, has done just that.

An abnormality in corn is to be understood, therefore, as a deviation from a highly artificial picture, a picture which, incidentally, many who know the plant only in the great corn-growing areas of the United States have to revise radically when they first encounter some of the bizarre varieties grown by primitive races in out-of-the-way places. The great frequency with which the *normal* plant occurs is a misleading thing.

1. Sexual Anomalies

In early stages of their development all flowers of the corn plant are essentially alike, and all have the initials of a pistil and three stamens. In the course of further development, there is ordinarily a suppression of one or the other of these sets of organs, so that the flower is ultimately imperfect. The regularity with which one type of flower develops in the tassel and the other in the ear shoot, and the frequency with which sexual irregularities occur in the terminal inflorescences in basal sucker branches, which share the characteristics of the main stem and of the ear branch, suggest some sort of physiological gradient determining the direction in which the development will go. The mechanism of this directive influence is not known, but the frequency with which the unexpected happens and the ease with which the ordinary course of events can be disturbed experimentally suggest a profitable experimental approach to the problem.

Functionally perfect flowers resulting from such derangements are probably infrequent, even though external appearances may seem to indicate that both sets of organs are fully developed. The anomaly more often takes the form of a sex reversal. An occasional pistillate flower, with its long silk, may be found in the tassel of almost any variety, and an occasional staminate spikelet may be found in the ear. In the latter case the abnormal spikelet is usually the pedicelled member of the pair. Frequently the reversed spikelets are found in some characteristic arrangement, as when the ear has a staminate tip or a staminate segment is inserted in the ear (Fig. 21). Such an occurrence can often be attributed to an environmental factor. For example, when corn plants are grown in the greenhouse in the winter, the imbalance of light and temperature may lead to the production of only pistillate flowers in both the lateral and terminal inflorescences. Since some varieties are much more amenable than others to this treatment, it is evident that genetic factors are also involved. Indeed, in some varieties, such as tunicate, tassel seed, and some dwarfs, the genetic factor is so strong that sexual aberrations appear in almost any environment in which the plant can grow.

2. *Vivipary*

Another anomaly, which has been mentioned in the literature under various names, consists of the production of small, vegetative, bulblike structures instead of the staminate spikelets (Collins, 1909). In a few instances, these have been removed and successfully planted to produce new plants. This behavior is essentially the same as aerial bulb production in many other plants. It occurs regularly in a few other grasses and sporadically in many others and is thought to be due to some environmental factor in certain cases. In the tassel of corn it is often found in several plants in some definite area in the field, and there is some indication that it may be caused by a fungus. (See Chapter XII, Section VII, 2, on Downy Mildews.)

Morphologically related to vivipary, but different in the way in which it functions, is the genetic anomaly known as "silky ear" (Fraser, 1933). Here a primordium which would ordinarily develop into a pistillate spikelet continues indeterminate growth for a time and produces a small ear (Weatherwax, 1935, pp. 51-52). A noninherited morphological parallel to this also occurs occasionally.

3. *Pod Corn*

Perhaps the best known and most controversial anomaly in the plant is *tunicate* or *pod corn*. The constant feature of this is the develop-

ment of the bracts of the pistillate spikelets to such an extent that they cover the mature grain and resemble the ordinary husks of the ear in texture. This character is controlled by a single dominant gene. The typical podded ears (Fig. 22) are found on heterozygous plants. The ears of the homozygous pod plants are rudimentary, or, when they develop to any appreciable extent, their spikelets are barren. Pistillate flowers are borne in the tassel, but ordinarily there is no viable pollen. In addition, there are many other atypical developments of the spikelets and vegetative parts (Collins, 1917; Mangelsdorf and Reeves, 1939; Weatherwax, 1950).

Stocks of pod corn are maintained by self-pollination of the heterozygous plants or by pollination with normal pollen. Their erratic behavior is attributed, in part, to the varying genetic backgrounds on which the tunicate character is superimposed.

A series of half-tunicate forms have also been discovered, in which the bracts surrounding the grains are longer than normal but shorter than those of the ordinary tunicate types. The genes responsible for these do not, however, affect other parts of the plant as does the tunicate gene.

The origin of pod corn is not known. Its wide distribution in both North and South America indicates that it has long been maintained, possibly as a curiosity, or that it has arisen more than once by mutation. It has been cited many times as the possible ancestor of cultivated corn, but there are serious objections to such a theory (Weatherwax, 1950. See also Chapter I, Section 5, d, this volume). For the present we prefer to regard it as only a hereditary monstrosity in which the responsible gene produces a profound change in the ordinary growth mechanism of the plant.

4. *Teopod Corn and Corn Grass*

Two other anomalies, which have appeared recently in experimental stocks, show some resemblance to pod corn in their basic character and lend some support to our interpretation of pod corn. One of these is known as *teopod* corn (Lindstrom, 1925) because of some superficial resemblance to both teosinte and pod corn. The other is known as *corn grass* because of its resemblance to wild grasses (Singleton, 1950).

In *teopod* corn the individual plant shows more than the normal amount of branching, and this results in a spectacular ear shoot with numerous small ears on branches of secondary, tertiary, or higher orders (Fig. 24). The ear (Fig. 25) resembles externally that of pod corn, but the conspicuous bracts between the grains prove to be the

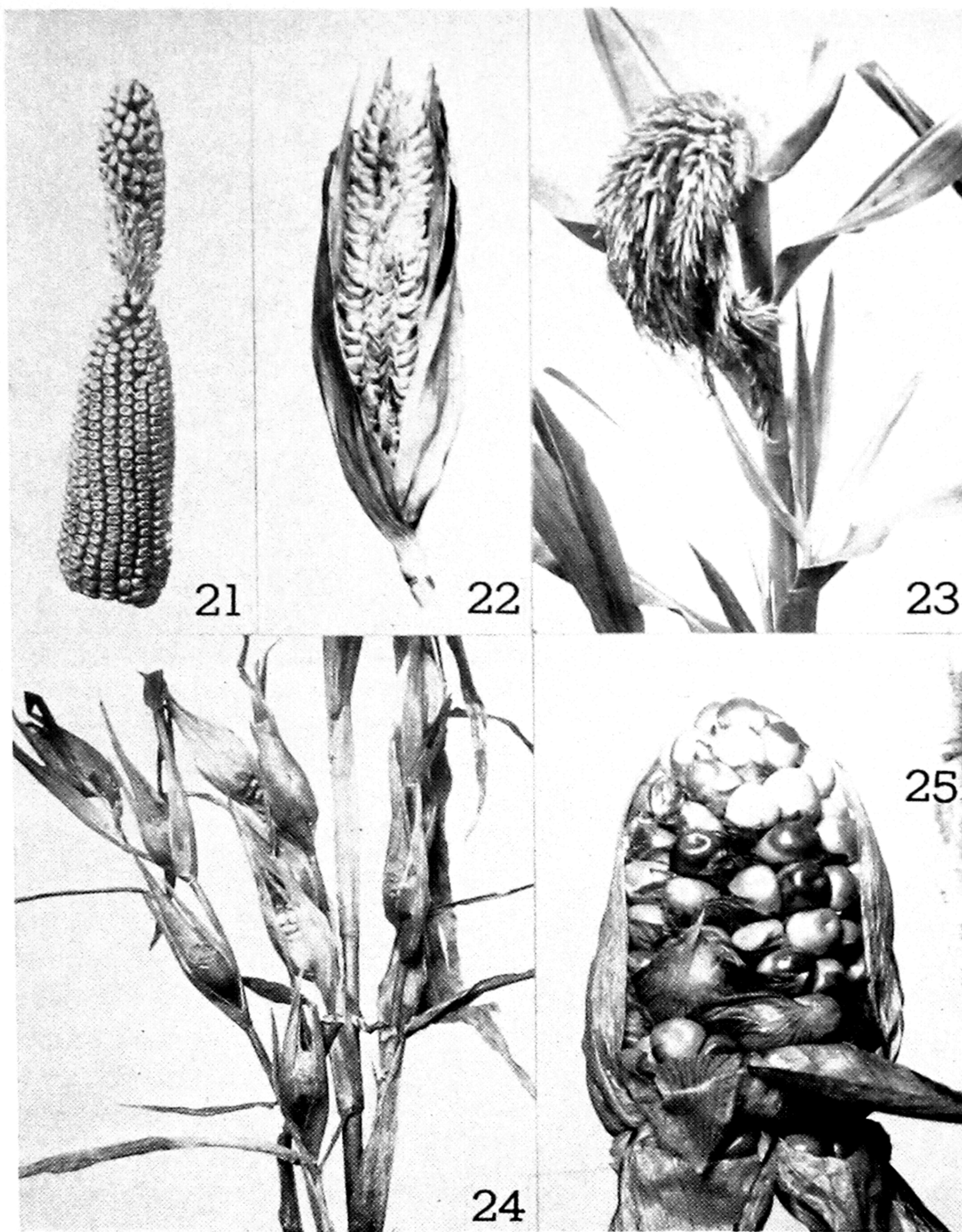


FIG. 21. Ear with staminate segment.

FIG. 22. Heterozygous tunicate ear.

FIG. 23. Tassel of homozygous plant of pod corn.

FIG. 24. Ear branch of teopod corn.

FIG. 25. Ear of teopod corn.

leaves which subtend the pairs of spikelets. The homologous leaves of the tassel are developed to the point where they resemble foliage leaves (Fig. 26; Weatherwax, 1929).

In corn grass (Figs. 27, 28) there is a similar development of the leaves subtending the pairs of spikelets, but the fruiting structure shows

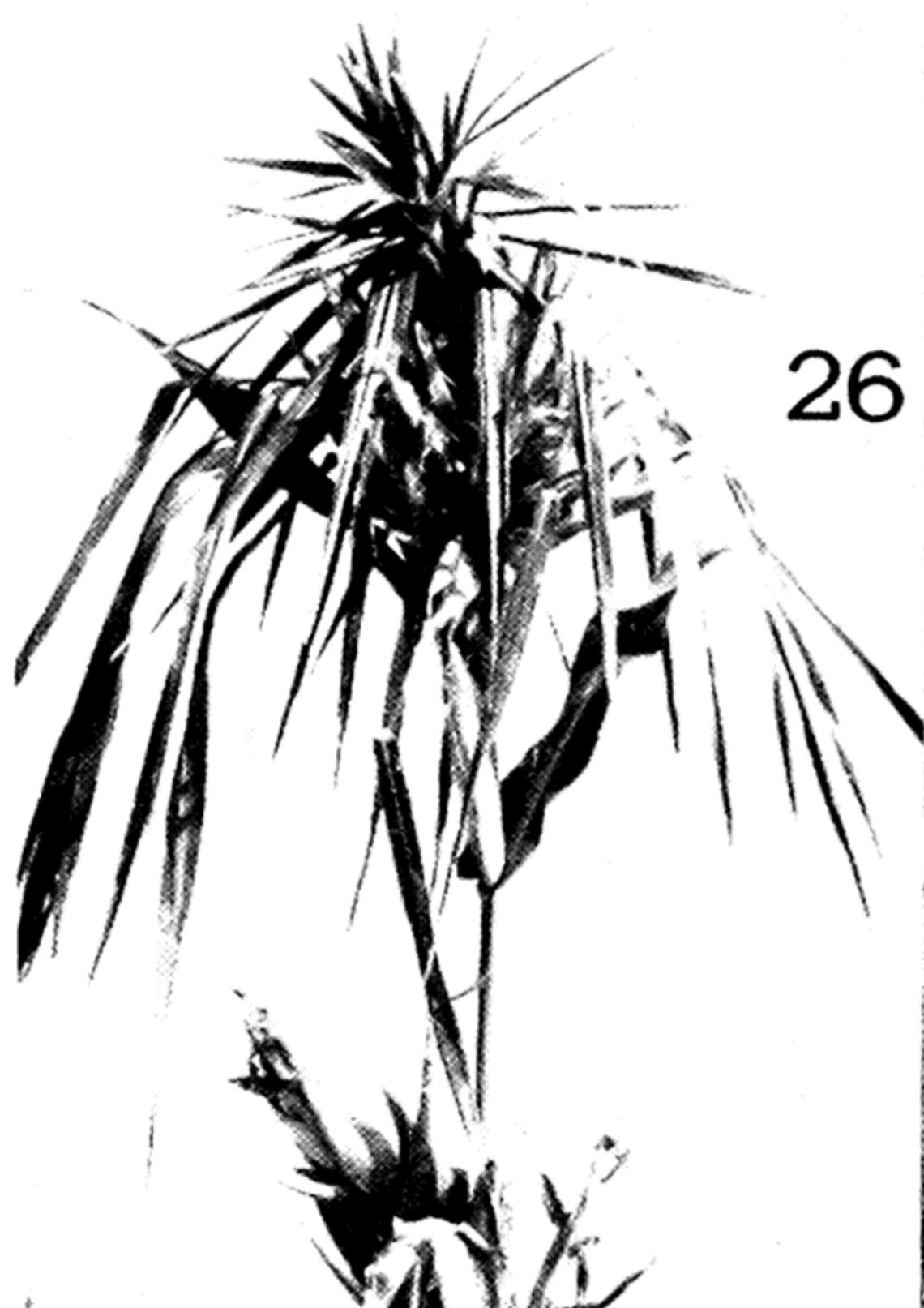


FIG. 26. Tassel of teopod corn.

FIG. 27. Habit of corn grass.

FIG. 28. "Ear" of corn grass.

little resemblance to an ordinary ear. The tassel is similar to that of teopod corn.

Teopod corn produces little or no viable pollen. Self-pollinations of corn grass have been made, but they would probably not occur under ordinary conditions without help. Both anomalous forms are ordinarily maintained by pollination with normal pollen.

The vegetative and genetic character of teopod corn and corn grass is so similar to that of pod corn as to suggest that all three are much alike in significance. There is in all three the same tendency toward male sterility and the same general disturbance of growth pattern which brings back some aspect of the full development of organs which were lost long ago in the evolution of the plant.

VIII. Anomalous Ears

Much of the unique character of the corn plant and the remarkable success of the plant breeder in dealing with it, both in historic and prehistoric times, are due to the plastic nature of the ear during development. This same plasticity is also responsible for the occurrence of several types of anomalies. Some of these are inherited; others can be attributed only to freaks of development.

1. *Fasciations*

One of the commonest of these anomalies consists of a flattening of the tip of the ear in various ways, often accompanied by some degree of branching. It is unfortunate that the term *fasciation* has been applied to these; it carries with it the literal meaning of a bundle of sticks and serves to keep alive the erroneous idea that the ear of corn arose through the phylogenetic fusion of simpler spikes. A true fasciation, as defined botanically, is simply an enlarged, flattened, and often branched structure which has the appearance of several fused branches. It often occurs in stems and other structures in which there is no suggestion whatever of an origin by fusion. Although the term is subject to this wrong interpretation, it is the only concise one that we have.

Fasciated ears appear in many forms (Figs. 29–31). The condition is inherited in a white pop corn known as “bear’s foot,” in a red variety whose short, conical ears resemble strawberries, and in some standard dent varieties of southern Mexico and Central America.

2. *Furcations*

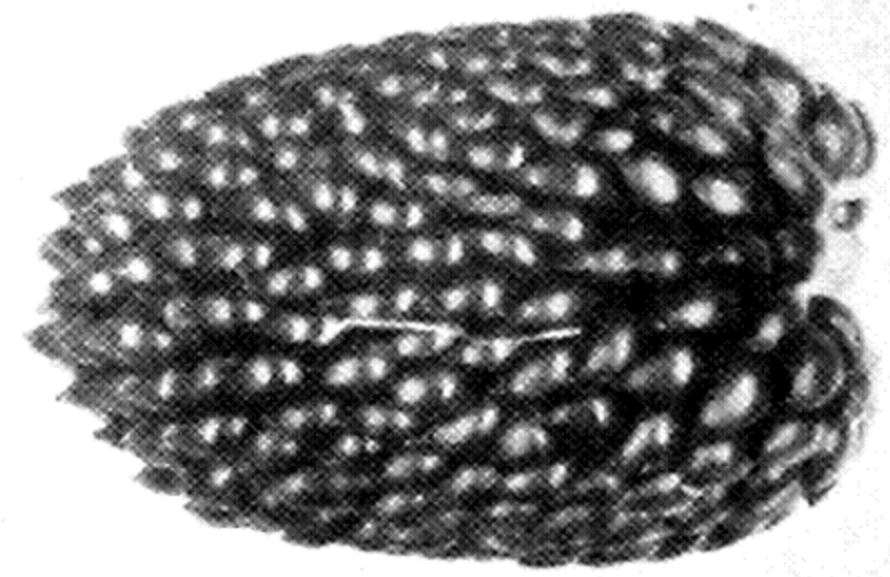
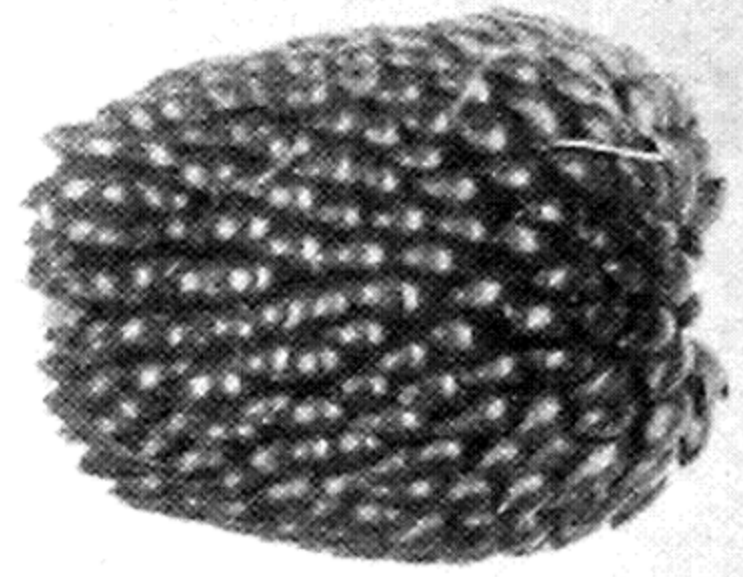
Ears deeply cleft into two or more parts may occur sporadically in any variety, possibly sometimes as a result of injury to the apical meristem as the ear is developing (Fig. 32). In some varieties of tropical



29



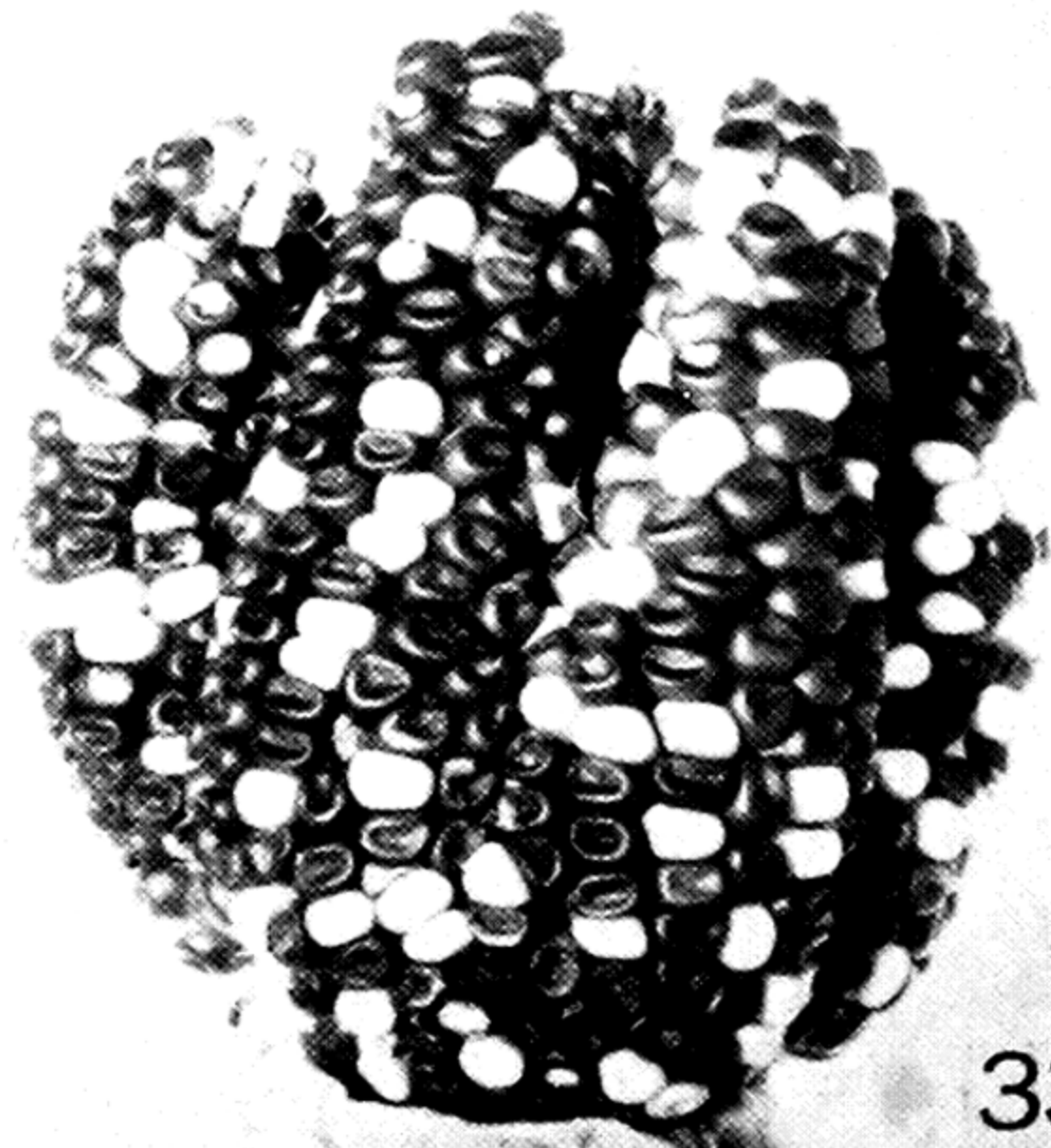
30



31



32



33

FIGS. 29, 30. Fasciated ears.

FIG. 31. Fasciated ear of strawberry pop corn.

FIG. 32. A noninherited type of ear furcation.

FIG. 33. Inherited furcation of ear of a Mexican variety.

America this character is hereditary and occurs so regularly that it is regarded as not at all unusual (Fig. 33).

3. Basal and Irregular Branching

Ears otherwise normal in appearance may have a whorl of branches around the base (Fig. 34). These branches, which usually have four

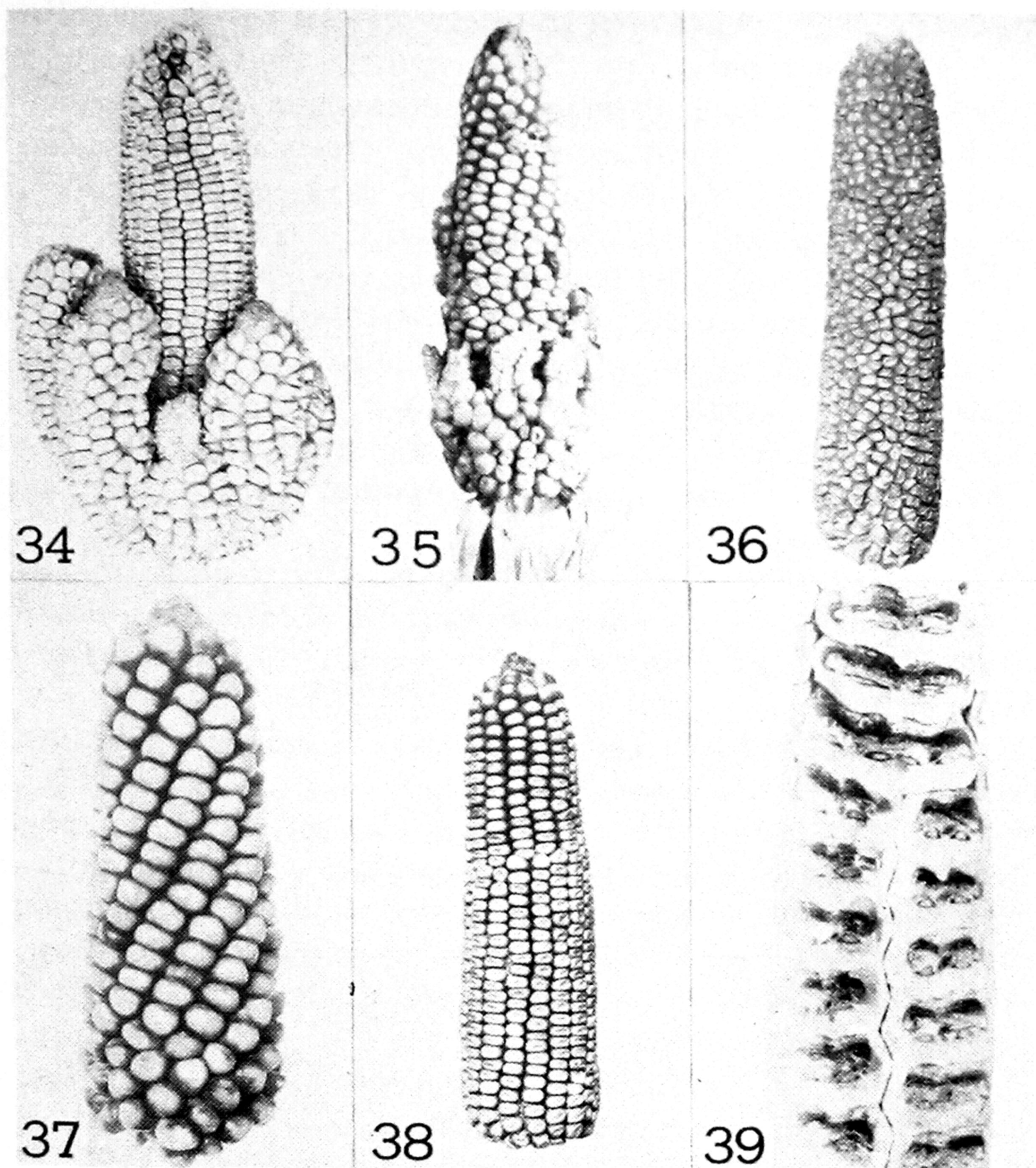


FIG. 34. Ear with whorl of basal branches.

FIG. 35. Ear with irregular branching (Guatemala).

FIG. 36. Ear of Country Gentleman sweet corn with no visible rows.

FIG. 37. Ear with spiral rows of grains (10 rows).

FIG. 38. Ear with 16 rows at base and 14 at tip.

FIG. 39. Cob of the ear shown in Fig. 38, with chaff removed to show true arrangement of pairs of spikelets.

rows of grains, may be regarded as the equivalent of the lateral branches of the staminate tassel, which were lost somewhere in the evolution of the ear. Structures resembling the whorled basal branches may be found rarely at higher levels anywhere on the ear (Fig. 35).

4. Irregularities in Rows of Grains

The most common irregularity in the rows of grains is seen in certain varieties, of which "Country Gentleman" sweet corn is the best

known example, in which each pistillate spikelet bears two grains instead of the usual one (Fig. 36; Kempton, 1913; Stewart, 1915; Weatherwax, 1917). Since there is no compensation for the extra grains in increased length of the cob, and they are closely crowded during development, many of them are pushed out of their regular positions, and frequently no rows are discernible externally. An ear of this sort can usually be identified by the fact that the extra grains, developing in the flowers which are usually aborted, are smaller than the normal ones and have their embryos oriented toward the base of the ear or turned to one side. Any other condition which causes the grains to develop in crowded conditions, or in which the spiral arrangement of the pairs of spikelets takes precedence over the longitudinal rows, is likely to produce the same visible effect.

Ears with the rows of grains running spirally will almost often be found to have 6, 10, 14, or some other number of rows *not in multiples of 4* (Fig. 37). In other words, such ears have an odd number of rows of pairs of grains.

When an ear has more rows at one end (usually the base) than at the other, the difference is two rows or some multiple of two (Fig. 38). Contrary to at least one published report (Collins, 1919), as rows are dropped between the base and the tip, they are dropped in pairs. The crowding of grains as they approach maturity will often make it appear externally that single rows had been dropped in two or more places, but a proper dissection reveals the true state of affairs (Fig. 39; Weatherwax, 1920).

5. Ears with Odd Rows

One of the classical quests of corn morphology has been to find an ear with an odd number of rows of grains. At first approach this would seem to be impossible because there is no way in which pairs can be added together to produce an odd number. Oral folk literature abounds in stories of fabulous prizes offered for a single ear with an odd number of rows. Solutions to the problem have been faked by carefully removing one row of grains from a young ear and allowing subsequent growth and crowding to close the gap.

A naturally inherited occurrence of ears with odd rows has recently been found to be due to the abortion of one member of each row of the pairs of spikelets (Hepperly, 1949). Whenever the gene for this condition is present, and the rows of pairs of spikelets appear in an odd number, the number of rows of grains will be odd. The surprising thing is that this does not happen more often; the suppression of one

member of the pair of pistillate spikelets is the normal thing in both *Tripsacum* and *Euchlaena*.

Another condition which may give rise to odd-rowed ears is seen in a variety cultivated by certain primitive Indians in the lowland jungles of eastern Peru and Bolivia and the adjacent parts of Brazil. The long, slender ears usually have from nine to twelve rows of grains, and nine rows occur often. Dissection shows that the pairs of spikelets (and grains) are arranged in spirals which are so steep that the right-hand grains of one longitudinal row of pairs intermesh with the left-hand grains of the adjacent row of pairs (Cutler, 1946, pp. 271–274). Since this occurs all the way around the ear, the net result is as many rows of grains as it has pairs of spikelets; and, since it is not unusual for an ear to have an odd number of rows of pairs, it is a common thing to find an odd number of rows of grain.

6. Significance of "Abnormal" Ears

During the long process of selection to which corn has been subjected it seems likely that a premium has been placed on large ears of the form that we now regard as normal or typical. The continued recurrence of abnormal forms may be attributed to several things. Only in the past half-century have the basic principles of heredity been well enough understood to enable us to conduct a systematic program for completely eliminating undesirable genes, and new types of abnormalities also continue to arise from time to time by mutation. Anomalies of ontogeny are largely beyond control or prediction.

Besides these there is a human factor which has largely been overlooked. The early chronicles of American natural history contain many accounts of magic agricultural rites and other primitive religious ceremonies based on deformed or unusual ears of corn, and it seems very probable that many of the hereditary anomalies, such as branched ears or ears with spiral rows of grains, have been preserved for their religious significance.

REFERENCES

A complete bibliography covering the materials of this chapter would be longer than the chapter itself. Only the works cited are listed here. For more comprehensive lists of publications the reader is referred to the longer and more recent papers listed below.

- BONNET, O. T. 1940. The development of the staminate and pistillate inflorescences of sweet corn. *J. Agr. Research* 60: 25–37.
 BONNET, O. T. 1948. Ear and tassel development in maize. *Ann. Missouri Botan. Garden* 35: 269–287.

- COLLINS, G. N. 1909. Apogamy in the maize plant. *Contribs. Natl. Herb.* **12**: 453-455.
- COLLINS, G. N. 1917. Hybrids of *Zea tunicata* and *Zea ramosa*. *J. Agr. Research* **9**: 383-396.
- COLLINS, G. N. 1919. Structure of the ear of maize as indicated in *Zea Euchlaena* hybrids. *J. Agr. Research* **17**: 127-135.
- COLLINS, G. N. 1925. The "metamorphosis" of *Euchlaena* into maize. *J. Heredity* **16**: 378-380.
- CUTLER, H. C. 1946. Races of maize in South America. *Botan. Museum Leaflets Harvard Univ.* **12**: 257-291.
- CUTLER, H. C., and ANDERSON, E. 1941. A preliminary survey of the genus *Tripsacum*. *Ann. Missouri Botan. Garden* **28**: 249-269.
- FARQUHARSON, L. 1953. Peculiarities in the embryology of *Tripsacum dactyloides*. *Proc. Indiana Acad. Sci.* **62**: 104.
- FARQUHARSON, L. 1954. Natural selection of tetraploids in a mixed colony of *Tripsacum dactyloides*. *Proc. Indiana Acad. Sci.* **63**: 80-82.
- FRASER, A. C. 1933. Heritable characters of maize. 44. Silky ears. *J. Heredity* **24**: 41-46.
- GERARDE, J. 1597. "The Herbal or General Historie of Plantes," p. 74. Norton, London.
- GUIGNARD, L. 1901. La double fécondation dans le maïs. *J. Bot.* **15**: 37-50.
- HACKEL, E. 1887. Gramineae. In Engler and Prantl, "Die Natürlichen Pflanzenfamilien." II, 2. Engelman, Leipzig.
- HEPPERLY, I. U. 1949. A corn with odd-rowed ears. *J. Heredity* **40**: 63-64.
- HITCHCOCK, A. S. 1922. A perennial species of teosinte. *J. Wash. Acad. Sci.* **12**: 205-208.
- KELLERMAN, MRS. W. A. 1895. Primitive corn. *Meehan's Monthly* **5**: 44.
- KEMPTON, J. H. 1913. Two-flowered spikelets in maize. *Bur. Plant Ind. Bull.* **278**.
- KIESSELBACH, T. A. 1949. The structure and reproduction of corn. *Nebraska Agr. Expt. Sta. Research Bull.* **161**.
- LAUBENGAYER, R. A. 1948. The vascular anatomy of the four-rowed ear of corn. *Ann. Missouri Botan. Garden* **35**: 337-340.
- LAUBENGAYER, R. A. 1949. Vascular anatomy of the eight-rowed ear and tassel of golden bantam sweet corn. *Am. J. Botany* **36**: 236-244.
- LINDSTROM, E. W. 1925. Heritable characters of maize. 21. A new dominant hereditary character, Teopod. *J. Heredity* **16**: 135-140.
- MANGELSDORF, P. C. 1948. The role of pod corn in the origin and evolution of maize. *Ann. Missouri Botan. Garden* **35**: 377-406.
- MANGELSDORF, P. C., and REEVES, R. G. 1939. The origin of Indian corn and its relatives. *Texas Agr. Expt. Sta. Bull.* **574**.
- MILLER, E. C. 1919. Development of the pistillate spikelet and fertilization in *Zea mays* L. *J. Agr. Research* **18**: 255-265.
- MONTGOMERY, E. G. 1906. What is an ear of corn? *Popular Sci. Monthly* **68**: 55-62.
- REEVES, R. G. 1946. Methods for studying the maize ear. *Botan. Gaz.* **107**: 425.
- SCHUMANN, K. 1890. "Neue Untersuchungen über den Blütenanschluss." Engelman, Leipzig.
- SINGLETON, W. R. 1950. Corn grass, a dominant monogenic spontaneous mutant, and its possible significance as an ancestral type of corn. *Genetics* **35**: 691-692.
- STEWART, A. 1915. The pistillate spikelet in *Zea mays*. *Science* **43**: 694.
- WEATHERWAX, P. 1916. Morphology of the flowers of *Zea mays*. *Bull. Torrey Botan. Club* **43**: 127-144.

- WEATHERWAX, P. 1917. The development of the spikelets of *Zea mays*. *Bull. Torrey Botan. Club* **43**: 483-496.
- WEATHERWAX, P. 1918. The evolution of maize. *Bull. Torrey Botan. Club* **45**: 309-342.
- WEATHERWAX, P. 1919. Gametogenesis and fecundation in *Zea mays* as the basis of xenia and heredity in the endosperm. *Bull. Torrey Botan. Club* **46**: 73-90.
- WEATHERWAX, P. 1920. A misconception as to the structure of the ear of maize. *Bull. Torrey Botan. Club* **47**: 359-362.
- WEATHERWAX, P. 1923. "The Story of the Maize Plant." University of Chicago Press, Chicago.
- WEATHERWAX, P. 1925. The reported origin of Indian corn from teosinte. *Proc. Indiana Acad. Sci.* **34**: 225-227.
- WEATHERWAX, P. 1926. Comparative morphology of the oriental *Maydeae*. *Indiana Univ. Studies* **73**.
- WEATHERWAX, P. 1929. The morphological nature of teopod corn. *J. Heredity* **20**: 325-330.
- WEATHERWAX, P. 1935. The phylogeny of *Zea mays*. *Am. Midland Naturalist* **16**: 1-71.
- WEATHERWAX, P. 1950. The history of corn. *Sci. Monthly* **71**: 50-60.

CHAPTER IV

The Cytogenetics of Maize

M. M. RHOADES

I. Introduction

Immediately following the rediscovery of Mendel's laws in 1900 the corn plant became a favored subject for genetical investigations. Among its desirable features is the separation of the male and female inflorescences which makes unnecessary the tedious emasculating required for controlled pollinations in many forms. Either selfing or crossing can be simply and rapidly done. Thousands of kernels can be obtained with relatively little expenditure of time or effort, since a single selfed or crossed ear contains several hundred kernels.

Another advantage offered by maize is the abundance of mutant characteristics. Different races exhibit wide phenotypic variations, and many of these have a simple genetic basis. By selfing individuals of open-pollinated varieties scores of recessive mutant genes are uncovered. These have long been carried in a heterozygous condition and are revealed only when they become homozygous through inbreeding. Maize has a wealth of mutant genes, with nearly 500 listed in the useful compilation by Weijer(1952).

Mutations have been found which affect aleurone, plant, pericarp, plumule, scutellum and endosperm colors, endosperm composition and development, plant height, chlorophyll formation (nearly 200 of these), structure of ear, tassel, leaf, and culm, modification of male and female inflorescences, carbohydrate metabolism, disease resistance, pollen and ovule abortion, pollen tube growth, etc. Some of the more interesting genes to the cytogeneticist are those controlling chromosome behavior and specific stages of mitosis. Among these is the asynaptic gene which affects meiotic pairing (Beadle, 1930, 1933), the sticky gene which causes the chromosomes to stick together as a confluent mass at metaphase and which produces an increased frequency of chromosomal aberrations and of mutations (Beadle, 1932c, 1937), and the polymitotic gene which induces the haploid nuclei of each quartet of spores to undergo a series of divisions in which the chromosomes pass undivided to one pole or the other, resulting in nuclei with less than the haploid

number (Beadle, 1931). There are genes which cause a failure of cytokinesis (Beadle, 1942d), one which affects the shape of the achromatic figure (Clark, 1940), one which controls chromosome coiling and produces a high percentage of unreduced megaspores (Rhoades, unpublished), and one which suppresses the onset of meiosis in both male and female flowers (Rhoades, unpublished). It is evident that genes not only determine the development of the plant as a whole but that the chromosomes themselves, which carry the genes, are also under genic control. Finally there are genes which determine the mutational events at other loci and genes which induce irreversible changes in cytoplasmic components.

There are relatively few dominant mutants; most of the mutant characters in maize are controlled by simple recessive genes and appear in monohybrid ratios. Some of the best analyzed genetic situations, however, involve the complementary interaction of a number of genes; among these are plant, aleurone, and scutellum color. Although inheritance in maize is prevailingly at the diploid level, there are 18 cases of duplicate factor, 2 of triplicate factor, and 1 of quadruplicate factor inheritance.

The maize cytogeneticist is indebted to those students whose investigations were purely genetic in nature, for only as the result of their painstaking and arduous labors has maize genetics been brought to its present high state. It was upon this genetic framework that the cytogeneticist added his contribution of the correlation of cytological observations with genetic data. Since this chapter deals with cytogenetics, many valuable contributions to the genetics of maize will not be considered. These important studies must await a full account of maize genetics. Certain aspects of cytogenetics only briefly mentioned in this review were more fully discussed in the paper by Rhoades and McClintock (1935). No attempt has been made to include all papers dealing with the cytogenetics of maize; rather we have tried to present a broad but not encyclopedic treatment. Since the cytogenetics of maize really began with the cytological identification of the different chromosomes, let us first discuss chromosome morphology.

II. Chromosome Morphology

The ten chromosomes comprising the monoploid or gametic number in maize are morphologically distinguishable by (1) their relative lengths, (2) distinctive chromomere patterns, (3) deep-staining knobs in characteristic positions, (4) location of the centromere (determining arm ratios), and (5) the degree of heteropycnosis in the chromomeres adjacent to the centromeres. These diagnostic features

are most clearly evident at pachynema when the chromosomes are found as elongated paired threads; it is this stage which has been so widely used in cytogenetic studies. Maize cytogenetics received its first great impetus when McClintock in 1929 reported that the ten chromosomes could be recognized by relative lengths, arm ratios, and knob positions at the prophase of the first microspore division. The longest member of the haploid complement was designated as chromosome 1, the second longest as chromosome 2, etc. Later, from her studies of the morphology of the pachytene chromosomes, which set the stage for a remarkable series of advances, it became apparent that the relative lengths of the ten chromosomes were in general the same at pachynema and at the first microspore prophase. There are, however, two changes in rank. Chromosome 5 is slightly longer than is chromosome 4 at pachynema and chromosome 8 is somewhat longer than is chromosome 7 (Fig. 1). As a consequence of its possessing the nucleolar-organizing region, a deep-staining somewhat reticulate body, chromosome 6 is always found associated with the nucleolus. It is the most readily identified of all the ten chromosomes.

The number of knobs varies greatly in different strains of corn. Knobs have been found in 22 different positions. Some strains have only knobless chromosomes, whereas in other races of maize a maximum of 16 knobs has been found in a single plant. When a particular knob is present on a certain chromosome, it is a constant feature of that chromosome and its inheritance is as precise as that of a mutant gene. Knobs are cytological markers in the same sense that mutant genes are genetic markers.

As is illustrated in Fig. 1, one or more knobs may be found on each of the 10 chromosomes. Longley (1938, 1939) in his extensive studies of knob position found that their locations along the lengths of the chromosomes were not random; there were no knobs in the proximal half of any chromosome arm. Some strains have knobs in the proximal halves of the long arms of chromosomes 2 and 3, but Longley's statement is otherwise true. Most knobs are internally located; of the 22 different knob positions only 3 are strictly terminal. The knobs in the short arms of chromosomes 3 and 4 have been described as terminal, but Longley believes them to be subterminal. Longley (1939) interprets the nonrandom knob distribution in the chromosome arms as indicating a knob-forming gradient along the chromosome arm: at its lowest level adjacent to the centromere, this knob-forming power becomes progressively higher in more distal regions until a maximum point is reached. It is unquestionably true that knobs are not randomly distributed, but there is no experimental evidence in support of Longley's hypothesis of

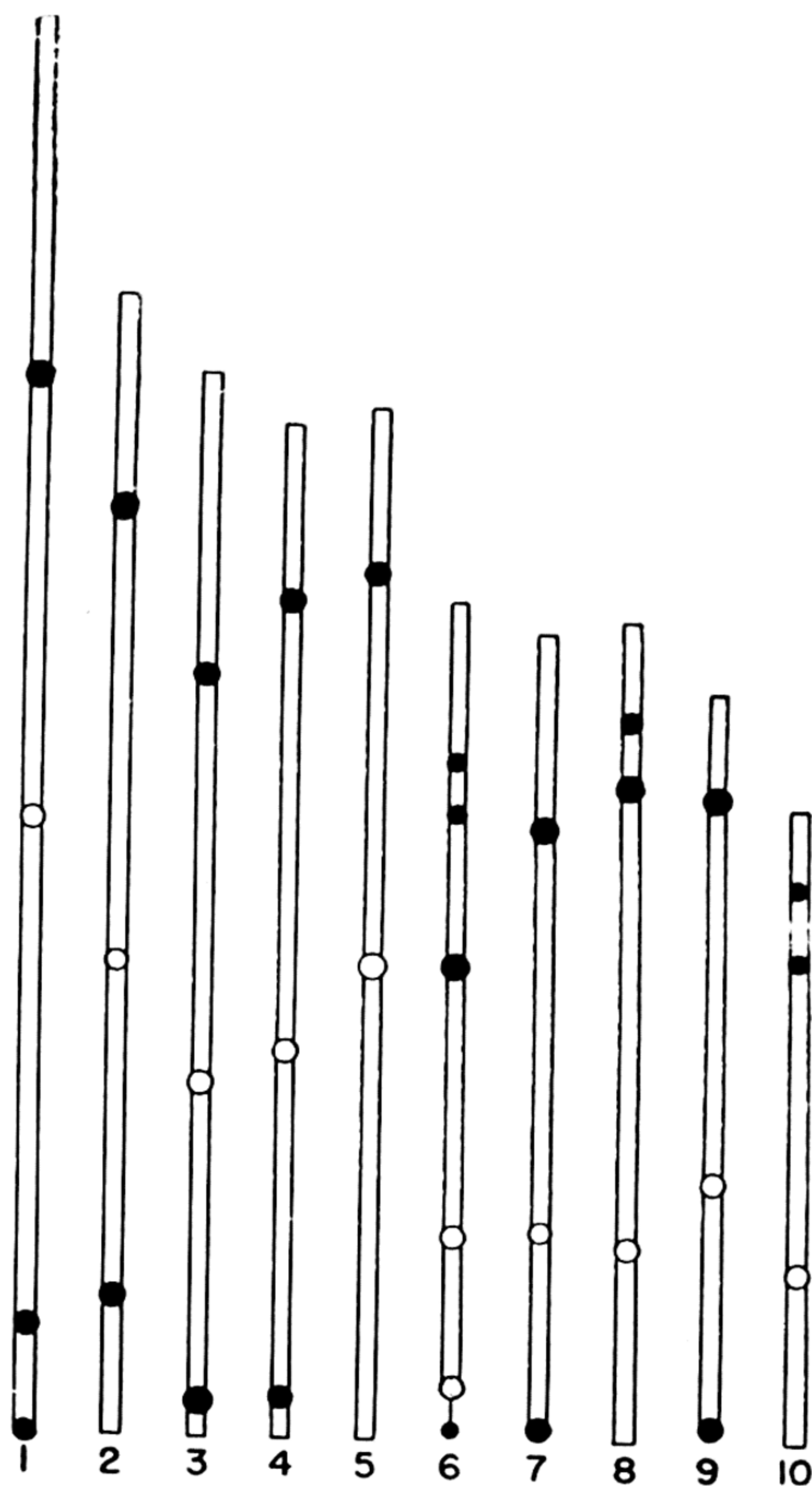


FIG. 1. Diagram showing relative lengths of maize chromosomes, location of knobs, and centromeres. The average pachytene lengths are from Longley (1939). The knobs (solid circles) are shown in their characteristic locations. Some strains of maize have chromosomes lacking in knobs, whereas other strains have many knobs. The centromeres are represented by clear circles. To aid in the identification of the different chromosomes, the following comments call attention to important features.

Chromosome 1. Longest of the complement. Knob or enlarged chromomere near end of short arm, and a small knob at end of short arm. Average length at mid-pachynema is 82.40μ . Ratio of long to short arm is 1.3:1.0.

Chromosome 2. Sometimes difficult to distinguish from No. 5 but differs from latter in ratio of arm lengths. The knob in long arm of No. 2 is further from the end than is the knob in long arm of No. 5. The regions adjacent to the centromere are more deeply staining than in No. 5. Length is 66.50μ at pachynema. In certain tester strains the arm ratio is 1.4:1.0, but in most races the arm ratio is 1.25:1.0.

Chromosome 3. A prominent knob lies approximately in middle of long arm and a smaller knob is situated 0.4 of the length of the long arm from the centromere (not shown in figure). Some strains have a small knob near middle of short arm. Length at pachynema is 62.00μ . Ratio of arms is 2.0:1.0.

Chromosome 4. Knob or enlarged chromomere near end of short arm. Differentiated from No. 3 by ratio of arms which is usually 1.6:1.0; in one strain, however,

a knob-forming gradient. In fact when a knob is shifted by a rearrangement to a new location near a centromere, there is no change in its appearance.

Knobs vary in size from those no bigger than a prominent chromomere to ones with a diameter several times that of the pachytene chromosome. They consist of accessory chromatin and the total length of the chromosome is increased by the linear dimension of the knob. Since knobs remain in a relatively contracted condition throughout the mitotic cycle (Morgan, 1943), their relative contribution to the length of a condensed metaphase chromosome is much greater than to that of a prophase chromosome with its uncoiled chromonemata. It has been stated that knobs are genetically inert. It is true that no obvious effects have been associated with the presence or absence of knobs, except for their possible role in the formation of extra chromosomal fibers at both meiotic anaphases when the abnormal form of chromosome 10 is present. It is clear that knobs are not essential for normal development, since some races have only knobless chromosomes. It may be questioned, however, if we are justified in concluding that knobs are genetically inert. Such a demonstration could come if isogenic stocks differing only by the presence or absence of knobs were compared. This is yet to be done. It is more likely that knobs are not wholly inert and that our experimental techniques have been too crude to detect their effects. The heteropycnotic, supernumerary B chromosomes are also considered to be inert or sub-inert, but Longley in his survey of knob number in dif-

the arm ratio is 2.0:1.0 because of pericentric inversion. Pachytene length is 58.78 μ .

Chromosome 5. Arms of almost equal lengths. Knob in longer arm. Pachytene length is 59.82 μ . Arm ratio is 1.1:1.0.

Chromosome 6. Attached to nucleolus by deep-staining nucleolar organizing region which is represented by a shaded circle. A small knob terminates satellite. Length at pachynema is 48.73 μ . Arm ratio is 7.1:1.0.

Chromosome 7. Region of the long arm adjacent to centromere is very deeply staining. Occasionally a strain has knob at end of short arm. Length is 46.78 μ . Arm ratio is 2.8:1.0.

Chromosome 8. Marked disparity in arm lengths. Regions on both sides of centromere are heteropycnotic but are less deeply staining than is the proximal region of the short arm of No. 10. Length is 47.48 μ . Arm ratio is 3.2:1.0.

Chromosome 9. Terminal knob often found at end of short arm. Proximal third of short arm composed of deep-staining chromomeres. Length is 43.24 μ . Arm ratio is 1.8:1.0.

Chromosome 10. Shortest chromosome of complement. Short arm has distinctive chromomere pattern with deep-staining chromomeres next to centromere and small tapering chromomeres at end. Knobs are rarely found, but two have been reported in long arm. Several strains have been found with a large, chiefly heteropycnotic segment attached to end of long arm (abnormal chromosome 10). Length of normal chromosome is 36.93 μ . Arm ratio is 2.8:1.0.

ferent races found a negative correlation between numbers of knobs and of B chromosomes—i.e., strains with high knob numbers had fewer B chromosomes than did those with a low number of knobs. This may indicate that knobs and B chromosomes play interchangeable roles in some metabolic function such as the synthesis or storage of deoxyribose-nucleic acid, which is abundantly found in both.

In his study of knob number and location in 74 varieties of maize from the United States and Mexico, Longley (1939) found knobs at 18 of the 22 known loci. There was a striking variation in the frequency with which certain knobs were encountered in these populations. The knob terminating the short arm of chromosome 9 was most frequently observed, occurring in 89.3 per cent of the plants; the knobs in the long arms of chromosomes 5, 7, and 4 were the next most frequent. The rarest knob was the one at the end of the short arm of chromosome 7, which was present in 0.6 per cent of the plants. Not only does knob size vary at different knob positions, but at any one location there is in different races a wide range in knob size. For example, chromosome 9 is knobless in some strains, but in other races it may have knobs ranging in size from a large chromomere to a large bulky body. However, the size of a knob in a given strain is constant and different-sized knobs can be used as cytological alleles.

✓ Knobs on nonhomologous chromosomes are often found paired or stuck together at pachynema to form a confluent mass of knob material. Occasionally knobs from several different chromosomes are involved. This association of knobs, however, is temporary, since it disappears during diplonema. S. R. Peterson (unpublished) found that non-homologous knob adhesion was not a random affair but involved certain knobs more frequently than others. She also observed that the non-homologous pairing of centromeres at pachynema was nonrandom. This pairing or adhesion of nonhomologous knobs and of centromeres suggests a nonspecific nature of the substance comprising these chromosomal organelles.

Not only is great variation found in knob size at specific knob loci but the nucleolar-organizing body of chromosome 6 also is not the same in all strains of maize. McClintock (1934) found that in certain strains it was the distal portion of the elongated organizer which developed the nucleolus. In other races the nucleolar-organizer had its main activity near the middle, and in still other strains the position of greatest activity was nearest the proximal end of the organizer. In the latter case the main body of the organizer would be included in the satellite. McClintock studied a translocation in which the organizer was partitioned between two chromosomes. Each of them possessed a

portion of the organizer body, and each portion was able at telophase to organize the matrical material into a nucleolus, although not with equal efficiency.

In any consideration of the significance of knobs on maize chromosomes mention must be made of the tripartite hypothesis of Mangelsdorf and Reeves (1939), which holds (1) that cultivated maize originated from a wild form of pod corn, (2) that teosinte is a recent product of the natural hybridization of *Zea* and *Tripsacum* which occurred after maize had been introduced by man into Central America, and (3) that new types of maize originating from this cross and exhibiting admixture with *Tripsacum* comprise the majority of Central and North American races. According to the hypothesis of Mangelsdorf and Reeves pure maize is without knobbed chromosomes, and it is true that varieties from the Andean region of South America which have no marked *Tripsacum*-like characters are knobless. Certain species of *Tripsacum* have many terminal knobs. They postulate that modern corn originated from an ancient cross between pure knobless maize and a many-knobbed *Tripsacum* species. If this be true, all of the knobs on the chromosomes of modern maize would be of *Tripsacum* origin. Although knobs are genetically inert and would in themselves have no phenotypic effect, it is assumed that segments of genically active *Tripsacum* chromatin accompanied the knobs when they were transposed to the pure maize chromosomes. It is these remnants of the *Tripsacum* genotype which are held responsible for the Tripsacoid features of modern maize. The majority of Central and North American races of maize with Tripsacoid characteristics have varying numbers of knobs; in general high numbers of knobs are positively correlated with characters which could have come from *Tripsacum* (Mangelsdorf and Cameron, 1942). There are, however, some exceptions. The Northern Flints of the United States which exhibit many *Tripsacum*-like characters have fewer knobs than any other group of U. S. varieties. Brown (1949) believes that knob number is a good indication of the amount of *Tripsacum* admixture, although it is not always a reliable criterion.

Although a considerable amount of indirect evidence has been found which supports the Mangelsdorf and Reeves hypothesis, it meets with a serious contradiction in that there is in the chromosome structure of present-day maize no indication of the rearrangements required for the transposition of the terminal knobs of *Tripsacum* to interstitial locations in the maize chromosomes (see Randolph, 1952). Cytogenetic mechanisms are known by which terminal regions could become internally situated, but these all involve gross structural alterations. If every internal knob on the maize chromosomes represents some kind of

transposition of chromatin from *Tripsacum*, it is difficult to understand why there is no indication of these ancestral rearrangements in modern maize.

Strains of corn from different parts of the world exhibit an amazing range in phenotypes owing to genic differences, but there is little evidence that gross chromosomal rearrangements have accompanied gene mutations in the evolution of the maize plant. That maize has a remarkably stable karyotype is indicated by the failure of Cooper and Brink (1937) to find any indication of reciprocal translocations in 55 strains of maize from Latin America and also by the failure of Rhoades and Dempsey (1953) to find evidence of either translocations or long inversions in their study of the chromosomal homology of 90 exotic races. Their method of detecting heterozygous inverted segments depended upon the occurrence of sufficient crossing over within the inverted segment to produce a significant increase in the percentage of aborted pollen. It is possible, therefore, that these exotic strains possessed chromosomes with inverted regions so small or located in regions of the chromosome where crossing over is so infrequent that they would not have been detected by the technique employed. Indeed there was some indication of small rearrangements, since significant differences in the amount of crossing over within a marked region were found in heterozygotes involving chromosomes from diverse races of maize. It is understandable why translocations or long pericentric inversions were not found in the exotic races. These structural changes arose sporadically in the past from time to time but had little chance of becoming incorporated in the population. When such rearrangements arose, plants possessing them would be heterozygous for the structural modification and consequently would have semisterile ears because of ovule abortion. It is unlikely that poorly filled ears would be used as seed stock by the discriminating American Indian.

The only known exception to the uniformity of chromosome homology is that of chromosome 10. There are two kinds of chromosome 10 (Longley, 1937). The usual or normal type is illustrated in Fig. 3. The rare and abnormal kind of chromosome 10 differs from the normal in the chromomere structure of the distal one-sixth of the long arm but more strikingly in having a large, chiefly heteropycnotic segment of chromatin terminally located on the long arm. Inasmuch as crossing over is reduced in the distal one-sixth of the long arm in plants heterozygous for abnormal 10, it is probable that this region with dissimilar chromomeres has some kind of structural change (Rhoades, 1952). The origin of the terminal segment of abnormal 10 can only be conjectured. Its lack of homology with other chromosomes of the comple-

ment is shown by its failure to synapse with them. Moreover the exceptional nature of abnormal 10 is demonstrated by its determining preferential segregation and the formation of neo-centromeres (see Section XI).

III. Polyploidy

Although the normal gametic complement consists of 10 different A chromosomes and diploids have two sets or 20 A chromosomes, many modifications of this number have been found. In the euploid series where entire sets are added or subtracted the number of sets ranges from one to eight. Monoploid or haploid plants, which have one set of chromosomes, arise spontaneously by the parthenogenetic development of unfertilized eggs. Much less frequent are the androgenetic monoploids, which come from the development of a sperm nucleus in the cytoplasm of the embryo sac. Chase (1949, 1951) found that the incidence of maternal monoploid plants was affected not only by the genetic constitution of the maternal parent but also, and this is truly surprising, by that of the pollen parent. The highest frequency came from crosses where both the female and male parents carried genes for high incidence of monoploidy. There is no evidence that the frequency of monoploids in maize is increased by delayed pollination or by irradiation of the pollen with X-rays, as has been reported for *Triticum*.

Monoploids are highly sterile because the meiotic segregation of the 10 unpaired chromosomes to the two poles results in the production of deficient spores which are inviable. The occasional kernels with diploid embryos found on the ears of monoploid plants pollinated by diploid males presumably come from the fortuitous inclusion of all 10 univalent chromosomes at one pole during meiosis. Somatic doubling may give diploid and fertile sectors in the male and female inflorescences. When diploid sectors arise in both the ear and tassel, with the consequent production of viable gametophytes, it is possible to obtain selfed progeny which are completely homozygous. A large number of these homozygous double-monoploid lines has been produced by Chase (1951) and Alexander (unpublished); it is possible that they may prove of value to the corn breeder. Although monoploid sporophytes are smaller than their diploid sibs, there is no striking external morphological difference between them. That this is characteristic of all members of the euploid series is understandable, since all have a balanced chromosomal complement and differ solely in the number of times the monoploid complement is replicated. Cell and nuclear size are smallest in monoploids and become progressively larger as the degree of ploidy increases.

In monoploid plants the 10 chromosomes are commonly found as univalents at diakinesis, but an occasional bivalent occurs. These have been interpreted as arising from legitimate crossing over between homologous segments in 2 different chromosomes—i.e., there are certain regions in duplicate in the monoploid set. Maize may be an ancient amphidiploid arising from the hybridization of two 5-chromosome species and could have homologous segments in duplicate. The 18 reported cases of duplicate factor, the 2 of triplicate factor, and the 1 of quadruplicate factor inheritance all suggest the presence of redundant loci. Although Sprague (1932b) demonstrated in his analysis of the inheritance of scutellum color that 15:1 ratios cannot be taken as unequivocal evidence of duplicate genes, there are other reasons for suspecting that there are duplicated segments in the architecture of maize germ plasm. Among these is the disproportionate distribution of mutant genes among the 10 chromosomes. The long arm of chromosome 9 has very few mutant loci, whereas the short arm with only one-half as much chromatin has more than 30 mutants. Similarly the short arm of chromosome 5 has only a fraction as many mutant genes as does the other arm, which is only slightly longer. The failure to find more mutants in the distal regions of the long arm of chromosome 4 and the paucity of mutants in chromosome 8 may be indicative of duplicated segments.

It should be pointed out, however, that this argument may be unsound. It is true that only four mutant alleles have been definitely placed in the short arm of chromosome 5, whereas several times this number lie in the longer arm, but this could well be due to the choice of tester stocks used in determining the linkage relations of unplaced genes. The *pr* locus in the long arm has been extensively used in the past to mark chromosome 5. Loci lying some distance from the centromere in the short arm would show little or no linkage with *pr*, and there would be no indication that they belonged in the same linkage group. McClintock's (1941a) studies with ring chromosomes composed of proximal segments of the short arm of 5 disclosed that in these regions there were several loci whose putative existence was indicated by the phenotypic appearance of tissue homozygous deficient for varying portions of the ring chromosome.

There is, furthermore, an alternative explanation for the occurrence of bivalent chromosomes in monoploid sporocytes. They may arise from illegitimate crossing over following the pairing of nonhomologous regions. McClintock (1933) showed conclusively that this kind of synapsis does occur and is extremely frequent when normal pairing partners are absent, as is true in monoploid maize. The discovery of

newly arising structurally modified chromosomes in the progenies of plants where nonhomologous pairing was known to occur is evidence of crossing over following nonhomologous synapsis. Although no definite conclusion can be drawn at this time, it is likely that the bivalents in monoploid sporocytes arise from both legitimate and illegitimate crossing over.

The triploids which arise in diploid populations usually come from the fertilization of a diploid or unreduced egg by a haploid sperm, but in one instance the male parent contributed the diploid number of chromosomes (Rhoades, 1936a). Diploid eggs and sperm result from some accident such as the nondisjunction of all the chromosomes in sporogenous divisions, during meiosis, or in one of the three mitoses of the female gametophyte. Triploids also occur regularly in the hybridization of diploid with tetraploid lines. The triploids found in diploid matings may arise spontaneously in normal material with a low frequency or may be of frequent occurrence in lines with genically induced disturbances of meiotic processes which produce unreduced nuclei. Beadle (1930) reported many triploids in the cross of asynaptic maize by haploid pollen where the formation of unreduced eggs was brought about by lack of pairing of the homologous chromosomes, and Rhoades (unpublished) also found many triploids in the progeny of plants homozygous for the elongate gene where unreduced eggs result from nondisjunction at the second meiotic division.

In triploids the chromosomes usually are associated at metaphase I as trivalents and less frequently occur as bivalents and univalents. A great majority of the spores of triploid plants are aneuploid with chromosome numbers ranging from 11 to 19 as a consequence of the random or near-random segregation of each set of 3 homologous chromosomes. Many of these aneuploid spores are unable to develop into viable gametophytes, and triploids characteristically have a high percentage of aborted ovules and pollen grains. When triploids were used as the pollen parent in crosses with diploids, McClintock (1929b) found a marked selection in favor of pollen grains with 10, 11, or 12 chromosomes; those with higher numbers were unable to compete successfully in achieving fertilization. The severe competition found among the male gametophytes was not evident in the reciprocal cross, where there was a wide range of chromosome numbers in the functional eggs. The different primary trisomes isolated by McClintock in the progenies of diploid by triploid crosses and their subsequent correlation with specific linkage groups marked the beginning of maize cytogenetics.

Tetraploid and octoploid plants were produced when the chromosome number was doubled and quadrupled by heat treatments applied

to young ears at the time of the first divisions of the young embryo (Randolph, 1932). Colchicine has proved relatively ineffective in maize in the induction of polyploid strains. Hexaploid plants have been produced by the union of unreduced $4N$ eggs and $2N$ sperm in crosses involving tetraploid plants homozygous for either the elongate or asynaptic genes (Rhoades and Dempsey, unpublished).

Tetraploid maize resembles the diploid in height and growth habit but has broader leaves, sturdier stalks, larger tassels, and ears and kernels of increased size. Randolph found that tetraploid strains were not as fertile as the diploid lines from which they were derived and that crosses between diploid and tetraploid lines were highly incompatible. More viable seed was produced when the tetraploid plant was used as the egg parent than in the reciprocal cross. Parthenogenetic diploids arising in tetraploid lines were much more fertile than their tetraploid sibs (Randolph and Fischer, 1939). Gilles and Randolph (1951) determined the relative frequency of quadrivalent and bivalent associations in a tetraploid strain at the beginning and at the end of a 10-year period during which the tetraploid line had been maintained by selecting the more vigorous and fertile plants. There were fewer quadrivalents and more bivalents at the end of the 10-year period than at the beginning. It appears that in selecting for vigor and fertility there was a concomitant selection for a gene or genes influencing the type of chromosome association. This shift from the quadrivalent type of pairing, believed to be diagnostic for autopolyploidy, towards the bivalent type characteristic for most allopolyploids raises doubt as to the reliability of using the presence or absence of quadrivalent association as a criterion for autopolyploidy or allopolyploidy.

Randolph (1935) found that because of irregularities in meiotic segregation not all of the offspring of tetraploid parents have 40 chromosomes. The number of chromosomes ranged from 37 to 42, although 40 was the most frequent class. This failure to breed true for chromosome number impairs the usefulness of tetraploid maize for cytogenetic studies. Nevertheless it is favorable material for certain problems such as, for example, studies on gene dosage (see Randolph and Hand, 1940).

In contrast to the euploid series, where each chromosome of the complement is present the same number of times, are the genically unbalanced aneuploid types. At the diploid level the addition to the normal complement of one or more chromosomes or fragments thereof gives hyperploids. Plants with a single extra chromosome are known as trisomes. Primary trisomes are those in which one member of the monoploid set is in triplicate while the remaining nine are in duplicate.

All of the 10 possible primary trisomes have been isolated in maize.

These have been derived chiefly from $n + 1$ gametes produced by triploids, although they have also arisen from nondisjunction in tertiary trisomes. All of the primary trisomes are smaller and less vigorous than their disomic sibs. Some can be recognized by characteristic phenotypic differences. This is true for trisomes 1, 2, 3, 4, 5, 7, and 8 but particularly for trisomes 5, 7, and 8. Plants trisomic for chromosome 5 have thicker, broader leaves with blunter tips, a more compact and stockier tassel, and a shorter stature than do disomes. The general appearance of plants trisomic for chromosome 5 is so pronounced that an accurate classification can be made in a segregating family for trisomic and disomic individuals. Plants trisomic for chromosome 7 can also be readily recognized by their stiff, narrow leaves with a leathery texture. Trisomes for chromosome 8 are more slender and flower several days earlier than their disomic sibs.

In primary trisomes only two of the three homologues are synapsed at pachynema at any one point, but exchanges of pairing partners occur so all three homologues are involved in the synaptic configuration. Einset (1943) found that the frequency of trivalent associations at metaphase I in different primary trisomes was positively correlated with the length of the chromosome. Since he reported that pairing at pachynema regularly involved all three chromosomes, it was assumed that desynapsis occurred in later prophase stages because of a failure to form chiasmata in some of the paired segments, thus giving rise at metaphase I to a bivalent and a univalent. It was argued that the longer chromosomes would on the average have paired segments of greater extent than those of shorter chromosomes and hence would present more opportunity for the formation of chiasmata which are held essential for post-diplotene association.

The different and diagnostic types of configurations found at meiosis in primary, secondary, and tertiary trisomes are intelligible on the assumption that pairing and chiasmata formation occur between homologous segments. Primary trisomes have chains of three and secondary trisomes, rings of three, whereas chains of five are typically found in tertiary trisomes at diakinesis.

The primary trisomes isolated by McClintock (1929b) from a spontaneously occurring triploid were extremely useful in cytogenetical studies. The association of 6 of the 10 linkage groups with specific chromosomes followed immediately. The way in which this was done is illustrated by McClintock and Hill's (1931) demonstration that the shortest chromosome of the complement carried the genes in the *R-g* linkage group. Different trisomes were crossed with plants carrying recessive mutant genes in the 10 linkage groups. The F_1 trisomic plants

were either selfed or backcrossed to recessive individuals. If the ensuing F_2 or backcross progenies gave 3:1 or 1:1 ratios, respectively, for a specific gene, it was evident that this gene was not located in the trisomic chromosome being tested. However, if trisomic ratios were obtained, it indicated that the gene in question was in the trisomic chromosome.

If a trisomic plant of AAa constitution is pollinated by recessive pollen, a 5:1 ratio of $A:a$ is expected if 50 per cent of the ovules are $n + 1$. Since less than half of the eggs are $n + 1$, owing to elimination of univalent chromosomes during meiosis, the observed ratio is less than 5:1, depending upon the frequency of univalents, but it is always strikingly different from 1:1 disomic ratios. Not only does the observed trisomic ratio depend upon the frequency of $n + 1$ ovules, but it is also influenced by the amount and kinds of crossing over between the gene and the centromere. If the locus of A is far enough removed from the centromere so that frequent multiple crossovers occur between it and the centromere, the assortment of the six chromatids, four with the dominant A allele and two with the recessive a , will approach randomness, and a ratio of approximately 4:1 instead of 5:1 would be produced if there were equal numbers of n and $n + 1$ gametes. Conversely if the gene is near the centromere, in terms of genetic units, there is no effect of crossing over on the ratio of dominant to recessive gametes. The segregation of the A - and a -bearing chromatids will be controlled by the disjunction of their respective centromeres, which is reductional in the first and equational at the second meiotic division, and a ratio of $5A:1a$ results with equal numbers of n and $n + 1$ spores. The effect of chromatid crossing over on trisomic ratios of several loci was shown by Rhoades (1933a) in his studies with chromosome 5 trisomes (see Section VI).

In a secondary trisome the extra chromosome is not a replica of one of the members of the monoploid set but is an isochromosome consisting of two identical arms. If the order of loci in chromosome 5 beginning with the distal end of the short arm is $a-b-c-d-e$ -centromere- $f-g-h-i-j-k$, the isochromosome derived from the short arm is $a-b-c-d-e$ -centromere- $e-d-c-b-a$ in constitution, and the other isochromosome would be $k-j-i-h-g-f$ -centromere- $f-g-h-i-j-k$. Since each of the 10 chromosomes can give rise to 2 isochromosomes, a total of 20 secondary trisomes is possible, but only the isochromosome composed of the two short arms of chromosome 5 has been found. This isochromosome was first found in 1933 (Rhoades) in a single plant in the progeny of an individual disomic for chromosome 5. An analysis of pachytene pairing clearly demonstrated the identical nature of its two arms. Two basic types of synaptic configurations were observed at pachynema. In the first type each arm of

the isochromosome pairs with a short arm of the two normal chromosomes 5. Pachytene pairing of this type gives rise to a ring of three at diakinesis. In the second type the isochromosome is not paired with the normal chromosomes 5, but its two homologous arms are synapsed with one another, producing a pachytene chromosome with its median centromere in a terminal position. At diakinesis the isochromosome forms a ring of one while the two normal chromosomes 5 are found as a bivalent. The manner of origin of this isochromosome is uncertain, but later studies by Rhoades (1940) with a telocentric chromosome 5 fragment consisting only of the short arm indicated that isochromosomes come from misdivision of the centromere. Instead of dividing normally in a plane parallel to the length of the chromosome it is believed that the centric region occasionally divides transversely in a perpendicular plane. When misdivision occurs in a normal chromosome, two isochromosomes are produced, one for each arm, whereas misdivision of the centromere of the telocentric chromosome gives rise to two centric regions, one of which has the two chromatids attached to it, thus forming an isochromosome, while the remaining portion of the centromere is devoid of chromatin. The fate of these naked centromeres is unknown. The telocentric chromosome was relatively unstable. Not only did it give rise to isochromosomes by misdivision of its centromere but it underwent a series of structural changes involving both losses and rearrangements. The instability of the telocentric chromosomes may account for the fact that they rarely are found in the normal complement of any organism. The only exceptions are the flagellates studied by Cleveland (1949). It was first shown by McClintock (1932) that both parts of a transversely broken centromere were capable of functioning. Although the gametic number of A chromosomes in natural populations is invariably 10, it is of interest that in experimental cultures the monoploid number has been increased from 10 to 11 by utilizing both portions of a fractured centromere (Rhoades, unpublished).

The secondary trisomes for the short arm of chromosome 5 were strikingly different in appearance from primary trisomes of this chromosome. Certain features which distinguish the primary trisome from disomes were exaggerated in the secondaries. They were short, stocky plants; the thick, broad leaves with extremely blunt tips had no tendency to assume a pendant position near their tips. On the other hand, the tassels of the secondaries were not markedly different from normal ones, although this was not true for those of primary trisomes.

In tertiary trisomes the extra chromosome is composed of parts of two nonhomologous chromosomes. Whereas the number of primaries is 10 and that of secondaries is 20, there is no limit to the number of

tertiary trisomes, since their constitution depends upon the contributions from the two parental chromosomes. This will vary widely, depending upon the position of the breakage points. The numerous tertiary trisomes in maize have been derived from plants heterozygous for translocations in which nondisjunction of the ring of 4 chromosomes at anaphase I results in a functional 11-chromosome gamete. Little cytogenetic work has been done with tertiary trisomes, but they have been used in the placement of genes within the cytological chromosome.

IV. B Chromosomes

In the early days of maize genetics there was some uncertainty about the true somatic number of chromosomes. Kuwada (1911, 1915, 1919, 1925), who was the first to make extensive counts, reported that the somatic number was not the same in different races of corn. He found that sweet varieties often had more than 20 chromosomes, whereas most field corn varieties had 20 chromosomes. Later studies by Fisk (1925, 1927), Longley (1924, 1927), Reeves (1925), Kiesselbach and Peterson (1925), and Randolph (1928a, b) confirmed Kuwada's finding that some strains had more than 20 chromosomes, although this was the number most frequently encountered. It became clear that 20 is the true diploid number and that numbers greater than this were due to the presence of a special kind of supernumerary chromosome which Randolph designated as a B-type in order to distinguish it from the members of the normal complement, which he called the A chromosomes. In somatic metaphases the B chromosomes differ from the A set by staining more intensely, by their club-shaped appearance, and by their peripheral location on the metaphase plate.

The B chromosomes found in diverse strains of corn and in teosinte all have a peculiar morphology which is quite dissimilar to that of any chromosome of the A set. Genetic data support the cytological observations that B chromosomes are not homologous with A chromosomes. Randolph (1941) in a test of 46 loci distributed among 17 different arms of the A chromosomes failed to find any indication that the B chromosomes possessed any of these loci. The origin of the B chromosome from any member of the regular complement is therefore unlikely. McClintock (1933) described in detail the morphology of the B chromosome at pachynema. Its length is slightly more than one-half that of chromosome 10, which is the shortest of the normal complement. There is either a terminal centromere or a short arm so minute that it often escapes observation. Beginning with the centromere, there is a heteropycnotic body which resembles the knobs of A chromosomes, next a lighter staining region containing several small but distinct

chromomeres which comprises about one-third of the pachytene length, then an elongated heteropycnotic region with several constrictions, followed by a bulging heteropycnotic region, and last a broken heteropycnotic segment composed of four distinct parts (Fig. 2).

Randolph (1941) made the important discovery that B chromosomes undergo nondisjunction at one of the microspore divisions. This phenomenon, which is responsible in part for the variation in the number of B chromosomes found in breeding experiments, is discussed further in Section VII. B chromosomes appear to be genetically inert or sub-inert, since they are not essential for normal growth and development. No phenotypic differences are observed in plants with low numbers of B chromosomes, but if the number is greater than 10 to 15, several abnormalities appear which increase in intensity with



FIG. 2. Diagram of the morphology of a B chromosome at pachynema. The centromere is represented as terminal. The segment with the small dots is euchromatic, and the heterochromatic regions are indicated by the large solid-colored areas. The arrow indicates the point of breakage in the T B-4a translocation described in Section VII.

greater numbers of B chromosomes. These include reduction in fertility, decreased vigor, defective kernels, aborted pollen, etc. Seed is rarely produced on plants with 25 or more B chromosomes. The highest number of B chromosomes found in a single plant was 34. The role of B chromosomes in cell metabolism remains obscure. Darlington and Upcott (1941) suggested that genetic function, possibly nucleic acid synthesis, could be inferred from population studies on numbers of B chromosomes where the equilibrium distribution indicated a positive selection. On the other hand, Ostergren (1945) proposed the interesting idea that B chromosomes were parasitic bodies.

Losses of segments of B chromosomes have given rise to derivative types of different size and morphology which Randolph has called the C, D, E, and F chromosomes. The C-type is somewhat shorter than the B, and the F-type consists only of a centromere with a small piece of chromatin.

V. Meiosis in Maize

Cytological observations of the meiotic stages have been chiefly confined to microsporocytes where the use of carmine or orcein smear preparations makes it a simple matter to obtain large numbers of flattened, well stained preparations of the various stages. Limited studies

of megasporogenesis, which have been confined to sectioned material, reveal that meiosis here is essentially the same as in microsporocytes. The following description of meiosis, largely taken from the account in Rhoades (1950), is entirely from smear preparations of pollen mother cells. Photomicrographs of all the important stages, except leptonema and zygonema, are shown in Figs. 4 to 6. Figure 3 is a camera lucida drawing of the pachytene cell (Fig. 4) in which the different chromosomes are identified.

Mitosis in the sporogenous cells of the anther is characterized by the marked elongation or attenuation, presumably by uncoiling, of the chromonemata. The prophase chromosomes in these premeiotic divisions

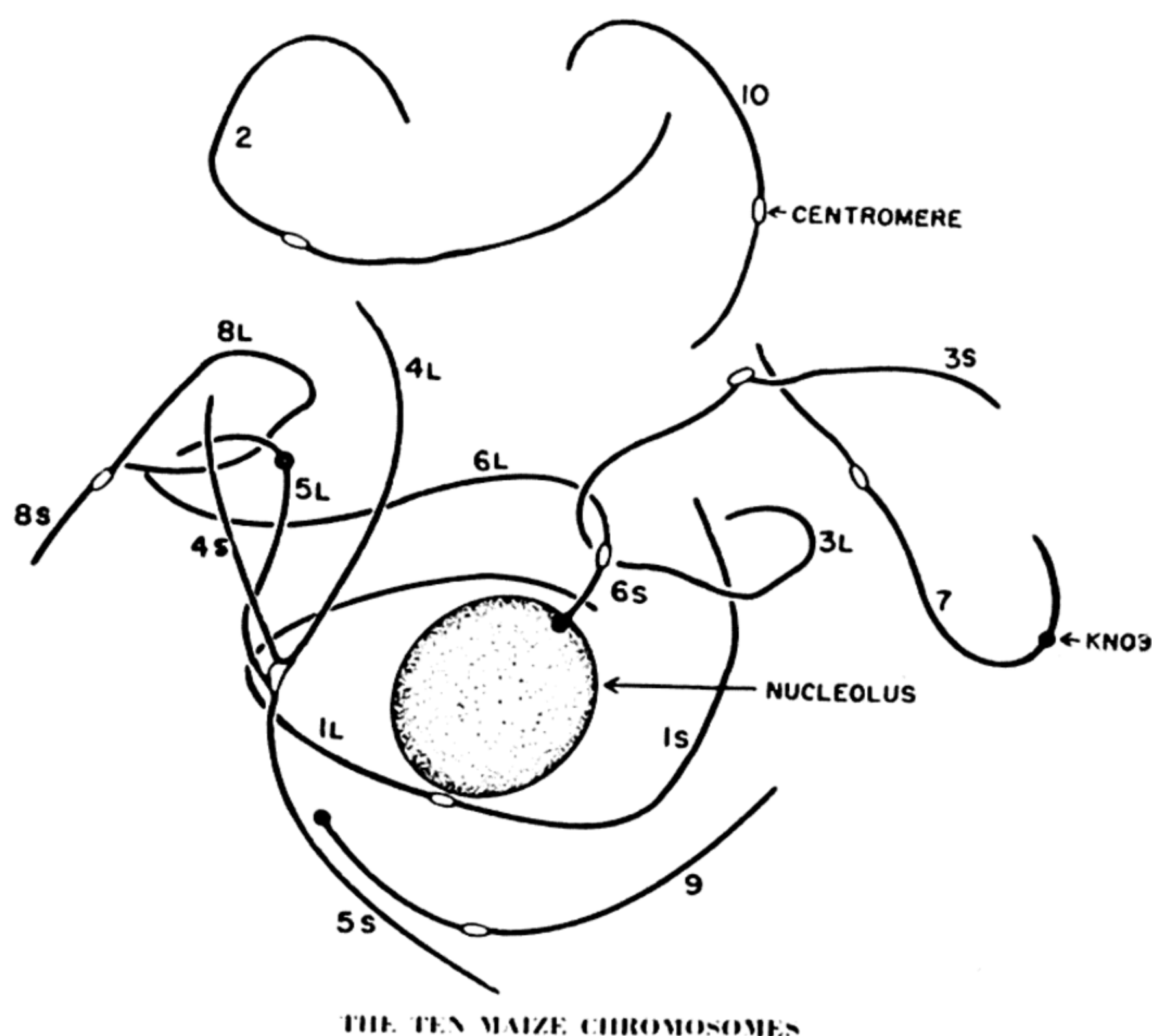


FIG. 3. Camera lucida drawing of the pachytene chromosomes of Fig. 4. Each bivalent chromosome is represented by a single line in order to simplify the diagram (From Rhoades, 1950).

are much longer than those in somatic cells. It is as if the chromosomes were being made ready for the onset of meiosis which finds the leptotene chromosomes as extremely long and slender threads—a condition which favors the gene-by-gene pairing beginning at zygonema.

It has not been ascertained whether the leptotene chromosome is single, but this is probable in view of the likelihood that crossing over between paired chromosomes occurs at early pachynema concomitantly with the formation of new chromatids. Whether single or not, the long and slender leptotene chromosomes consist of numerous, small but distinct chromomeres joined by fine, thread-like connections. The large heterochromatic knobs are found in their characteristic positions along

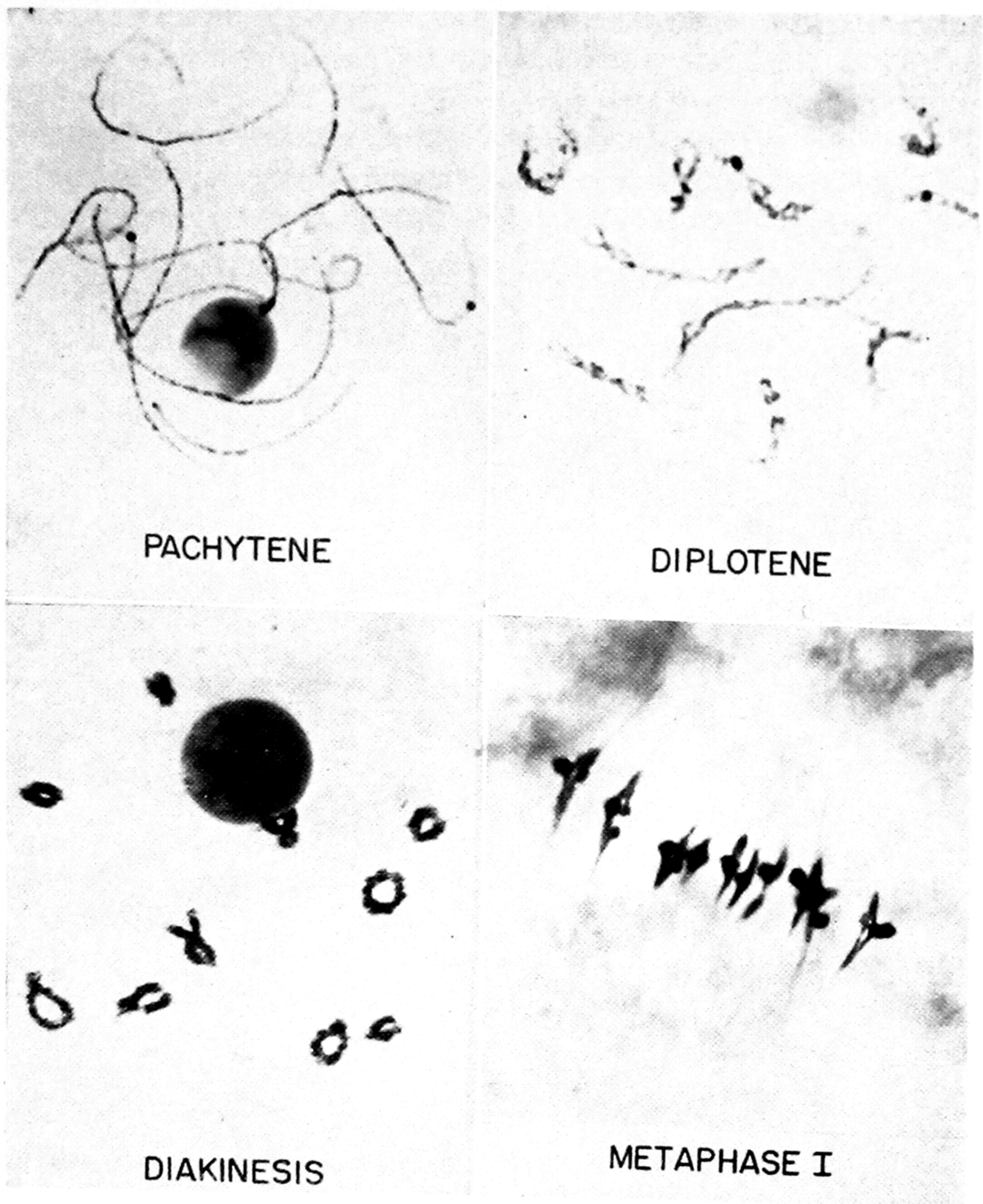


FIG. 4. Photomicrographs of meiotic stages in microsporogenesis. Pachynema to metaphase I. All are carmine smear preparations. The metaphase I is exceptional in that the chromosomes are less contracted than usual. See text for description of these stages. The beautiful pachytene figure is from a slide prepared by Dr. D. T. Morgan, Jr.

the chromonemata. In an investigation including many different genera Cooper (1952) reported that, at the time the meiocytes were at leptotema, the tapetal cells of the anther secreted globules rich in deoxyribose-nucleic acid which moved into the locule of the anther, where they first became closely associated with the nuclei of the meiocytes and later were included within these nuclei. Although his studies with maize were not as complete as those with other genera, it is likely in

maize that tapetal DNA becomes incorporated into the meiotic chromosomes and may indeed provide chromatin necessary for gene reduplication.

The chromonemata at zygonema are usually drawn into a tight knot next to the nucleolus. Chromosome structure in the synizetic knot is difficult to observe. However, the paired nature of the free arms occasion-

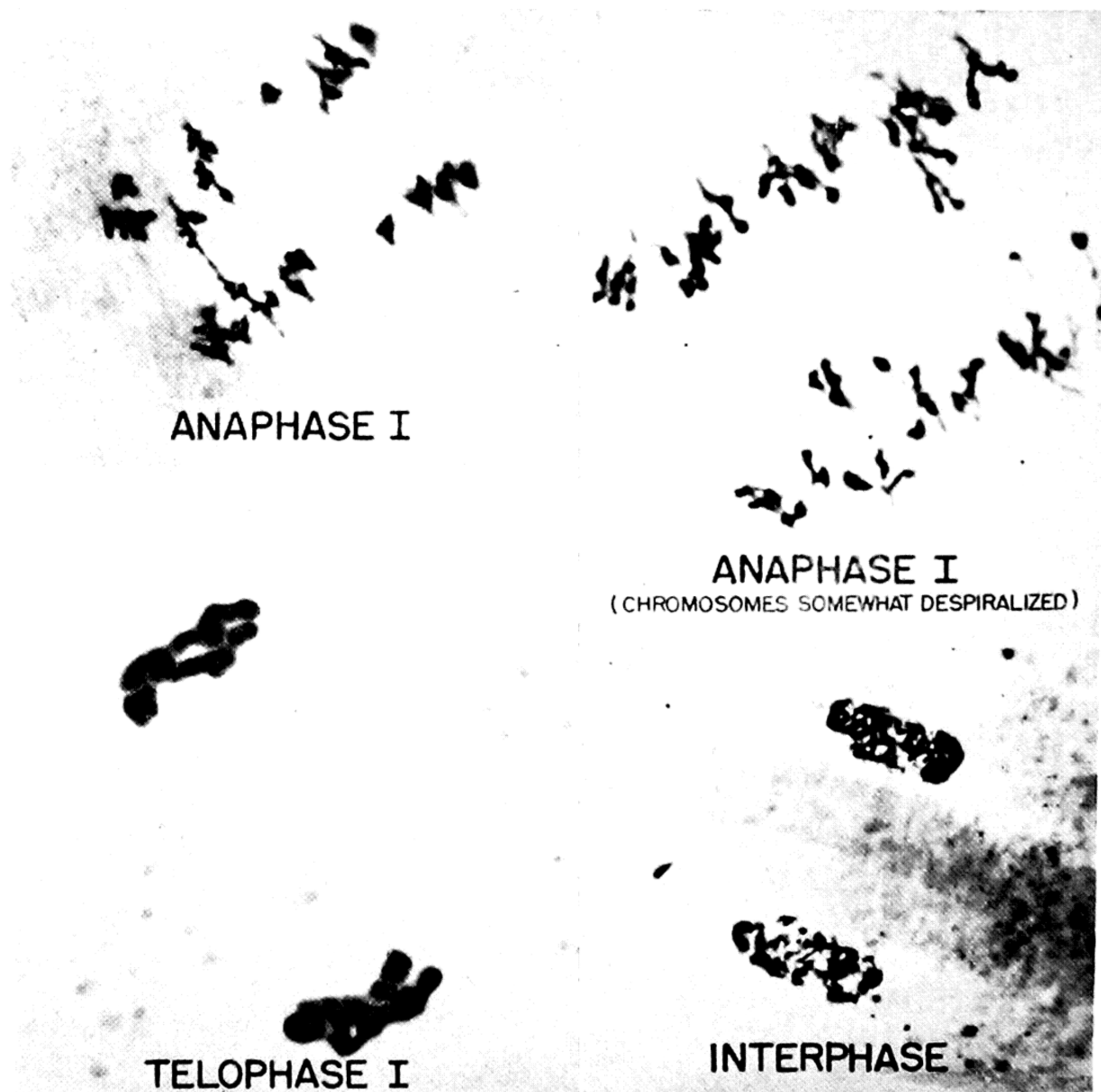


FIG. 5. Photomicrographs of microsporogenesis from anaphase I to interphase. In the cell at upper left are two disjoining dyads still connected by a persistent chiasma. The other dyads have fallen apart. The formation of the cell plate can be seen at interphase. See text for description.

ally found protruding from the chromatin mass reveals that synapsis has occurred.

When pairing occurs between chromosomes it usually is initiated at the ends, although it does not necessarily begin at any one point. The centromeres do not play a dominant role in initiating pairing. Once synapsis has begun it progresses in a zipper-like manner along the chromosome. The nature of synaptic forces was studied by McClintock

(1933) in normal, aneuploid, and structurally dissimilar maize plants. Chromosomes tend to associate 2 by 2 in the prophase of meiosis. It is the attraction between homologous regions which brings about the movement of homologous parts toward one another and which is responsible for orderly pairing, but there is a more powerful tendency for all parts of chromosomes to be associated 2 by 2 regardless of

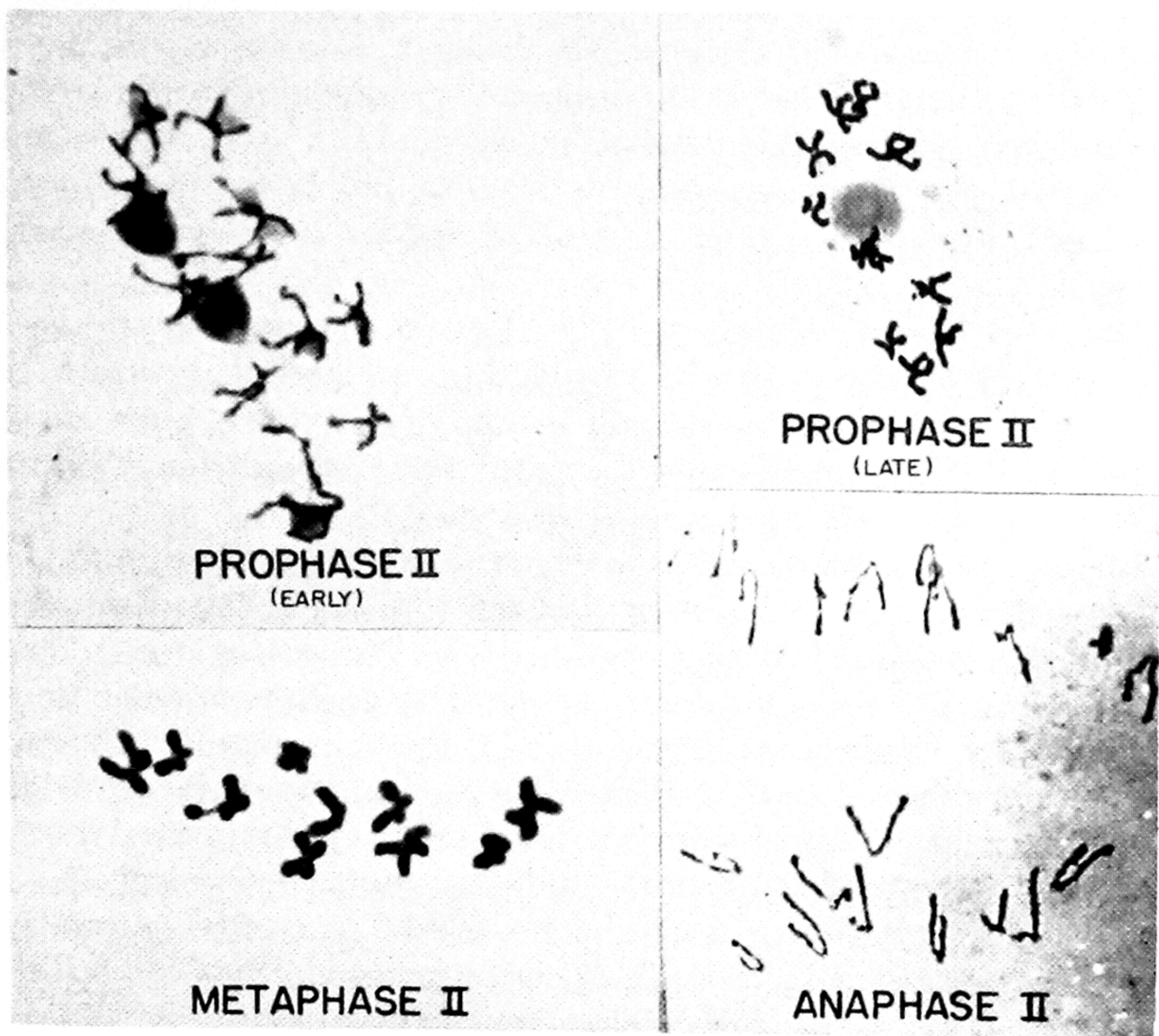


FIG. 6. Photomicrographs of meiotic stages from prophase II to anaphase II. The monads in this anaphase II are much more extended than is normally the case but otherwise this is an excellent preparation. See text for discussion.

homology. If the two chromosomal complements of a diploid are structurally identical, then synapsis, with rare exceptions, occurs only between homologous regions, but in unbalanced types and in structural heterozygotes the tendency for a paired association is so great that it often leads to the synapsing of nonhomologous segments if homologous parts are not present or are not immediately available.

Nonhomologous pairing is very common in monoploid sporocytes, where each chromosome is represented singly. It is also frequently observed in aneuploid types such as primary trisomes where at any one level one of the three chromosomes cannot be homologously paired

because synapsis involves only two of the three homologues. Lacking homologous regions with which to pair these univalent regions may undergo nonhomologous pairing. In translocation heterozygotes nonhomologous pairing is often found because of a conflict between the forces of homologous attraction and that producing 2 by 2 associations. Synapsis may begin at the ends between homologous segments of all four arms of the quadripartite configuration and progress toward the points of interchange in a zipper-like fashion. The pairing in one arm may continue beyond the region of homology and bring nonhomologous segments into a paired association, even though homologous segments are present. In inversion and deficiency heterozygotes, especially those involving short segments, nonhomologous pairing is frequently observed.

Regions nonhomologously associated at pachynema usually become dissociated at diplonema without having undergone crossing over. However, a number of new chromosomal types have been observed whose constitutions suggest that they may have arisen from illegitimate crossing over between nonhomologous segments.

At pachynema the paired homologues have emerged from the chromatin mass, and it is at this stage that the 10 pairs of chromosomes can be most readily identified (see Section II, on chromosome number and morphology for the diagnostic features). The pachytene pairs may be designated as tetrads since they consist of four chromatids. The paired homologues are relationally coiled, but there is no unequivocal evidence of major or minor coils at this time. Pachytene chromosomes are much shorter than those of leptonema, and this contraction continues progressively through the prophase stages until the relatively condensed metaphase I tetrad is formed. It is highly probable that coiling of the chromonemata is responsible for the gradual shortening.

Chiasmata are first evident at diplonema when the paired homologues open out to form loops and nodes. Most of the nodes represent chiasmata, which many geneticists believe arise from previous genetic crossing over, but some are due to a twisting of the paired chromosomes. It is not an easy matter to determine the correct number of chiasmata, although a few attempts have been made. Darlington (1934) reported that the average number of chiasmata per bivalent was 2.7 at diplonema and 2.5 at diakinesis, whereas Beadle (1933), working with a different strain, found an average of 3.7 chiasmata at diplonema but only 1.8 at diakinesis. It is possible that this discrepancy stems from differences in interpretation, since a half twist could be taken to be a chiasma. There is little terminalization of chiasmata toward the free ends. Although some bivalents at diakinesis and metaphase I have proximally located

chiasmata, most of them are concentrated near the distal ends. This is in agreement with the more frequent occurrence of crossing over in distal regions.

The transition from diplonema to diakinesis is a gradual one marked by further contraction and deeper staining. The large nucleolus has not noticeably changed from pachynema to diakinesis, but at the end of diakinesis it disappears as the nucleolar substance enters the chromosomes and contributes to the matrix of the deep-staining metaphase bivalents (McClintock, 1934). During prometaphase the nuclear membrane breaks down, the spindle is formed, and the tetrads move onto the spindle, with the two homologous centromeres of each tetrad lying on opposite sides of the equatorial plate (co-orientation). Polar views of metaphase I in sectioned material disclose that the bivalents are not peripherally arranged on the spindle plate but are uniformly distributed throughout. The number and location of chiasmata in the two arms determine the shape and appearance of the metaphase I bivalent. The half-spindle or chromosomal fibers which are formed by the centromeres control the anaphase I movement of the chromosomes. Separation of the tetrad into two dyad chromosomes begins at anaphase. The centric regions of each dyad move poleward at anaphase I and the chiasmata are unraveled. In Fig. 5 two separating dyads are connected by a persistent chiasma while the others have freely disjoined. A dyad consists of two chromatids, each made up of two arms; therefore it appears at anaphase as a double V if the centromere is near the middle or a double J if the centromere is more terminally located. The two chromatids of a dyad share a common undivided centromere. The four arms do not lie closely appressed during anaphase I but diverge as if they were mutually repelling one another. This repulsion between the four arms of a dyad is particularly evident at prophase II.

Each bivalent or tetrad at metaphase I is composed of four chromatids, of which two are derived from the maternal and two from the paternal chromosome. In maize the first meiotic division is reductional for the centromere regions, i.e., the centromere of sister chromatids a and a' disjoins to one pole while the centromere of the b and b' chromatids passes to the other pole. Since this division is reductional for the centromere, it follows that it is also reductional for the paternal and maternal pairs of chromatids out to that point where the first crossover occurs involving two nonsister chromatids, e.g., chromatids a and b . The first division will therefore be equational for the distal portions of the two crossover chromatids. The second division is reductional for those segments equationally segregated in the first division.

Direct cytological evidence that the first meiotic division is reduc-

tional for the centromere was first provided by McClintock (1933), who studied the anaphase I disjunction of a heteromorphic pair of chromosomes. One of the chromosomes was telocentric, consisting only of the short arm of chromosome 10; the other was a normal 10. If anaphase I were equational for the centric region, the two dyads passing to opposite poles would be identical, with each having two short arms and one long arm of chromosome 10. However, if reductional disjunction occurs at anaphase I, one of the dyads would consist of two short arms and the other of two chromatids each with a long and a short arm. She observed only the latter type of disjunction. It should be noted that the behavior of univalent chromosomes is an exception to the rule that anaphase I is reductional for the centromere, since they may divide equationally in the first meiotic division.

At late anaphase I the matrix material investing the chromonemata swells and appears as a light-staining substance in which the deeper-staining chromatin can be seen. By telophase the four arms of each dyad are so contracted that the dyad consists of four spherical masses of chromatin. The matrical material from the various dyads becomes a confluent mass as the dyads are grouped together at the pole. During interphase the chromonemata become greatly extended. Interphase is of too short duration to allow the formation of a typical metabolic nucleus with a single nucleolus, although the anastomosing of the matrical material causes some dispersion of the chromonemata. A cell plate is formed at the end of the first division dividing the pollen mother cell into two daughter cells each with 10 dyad chromosomes.

At early prophase II the long X-shaped dyads are partially or completely embedded in the confluent light-staining matrical substance. The chromosome arms become progressively shorter in later prophase stages, and the coiled nature of the chromonemata is often plainly visible. The dyads become more deeply stained as the matrical material is incorporated into the chromosomes. By metaphase II the compact dyads consist of four spherical masses of chromatin resembling those of telophase I, save that in the latter the matrical substance loosely invests the chromatin.

Prior to metaphase II the nuclear membrane disappears. A spindle develops upon which the dyads become oriented with the still undivided centromere lying on the equatorial plate (auto-orientation). The centromere of each dyad now becomes functionally double; chromosomal fibers arise from each chromatid and they pass to opposite poles during anaphase II.

The anaphase II chromosomes or monads appear as single V's or J's as contrasted to the double V's or J's of the anaphase I dyads. At late

anaphase II the matrical material around each chromosome is sloughed off and the ten monads at each pole at telophase II are connected by this coalescing material. A cell plate arises between the daughter nuclei, and the second meiotic division is now completed. Each of the four chromatids of the metaphase I tetrad has been distributed to one of the four haploid spores formed by the two meiotic divisions.

The only notable difference between micro- and mega-sporogenesis is that in the former four functional microspores are formed, whereas in the latter only the inner member of the linear set of four megaspores gives rise to a functional gametophyte.

VI. Crossing Over in Maize

In this account of crossing over no attempt will be made to illustrate how the linkage maps shown in Fig. 7 were constructed. This procedure is too well known to bear repetition. Instead we will discuss some of the illuminating researches which have been made with maize on the mechanism of crossing over.

1. Cytological Demonstration of Genetic Crossing Over

Genetic data on crossing over are explicable on the assumption that an actual exchange of segments occurs between the paired chromosomes, but it was not until 1931 that Stern working with *Drosophila* and Creighton and McClintock with maize obtained proof of the correlation between cytological and genetic crossing over. The cytogenetic demonstration in maize is as follows. Certain strains have a large, easily recognizable knob on the end of the short arm of chromosome 9, whereas other strains have a chromosome 9 which is knobless. In the reciprocal translocation T 8-9a, the interchange point in chromosome 9 is in the long arm. The presence or absence of both the knob and the translocation point afford two cytologically detectable markers on chromosome 9 which are constant features of those chromosomes which possess them and whose inheritance in subsequent generations can be followed with precision. The recessive genes yg_2 , c , and wx lie in the short arm of 9 between the translocation point and the terminal knob. The yg_2 locus is close to the knob, while wx is nearest the translocation point. Individuals were obtained heterozygous for the terminal knob, the translocation point, and the recessive genes located between the two cytological markers. These plants were testcrossed by structurally normal individuals carrying the recessive alleles and having knobless chromosomes 9. The ensuing progenies were classified for genetic crossovers between the yg_2 , c , and wx loci; both crossover and noncrossover plants

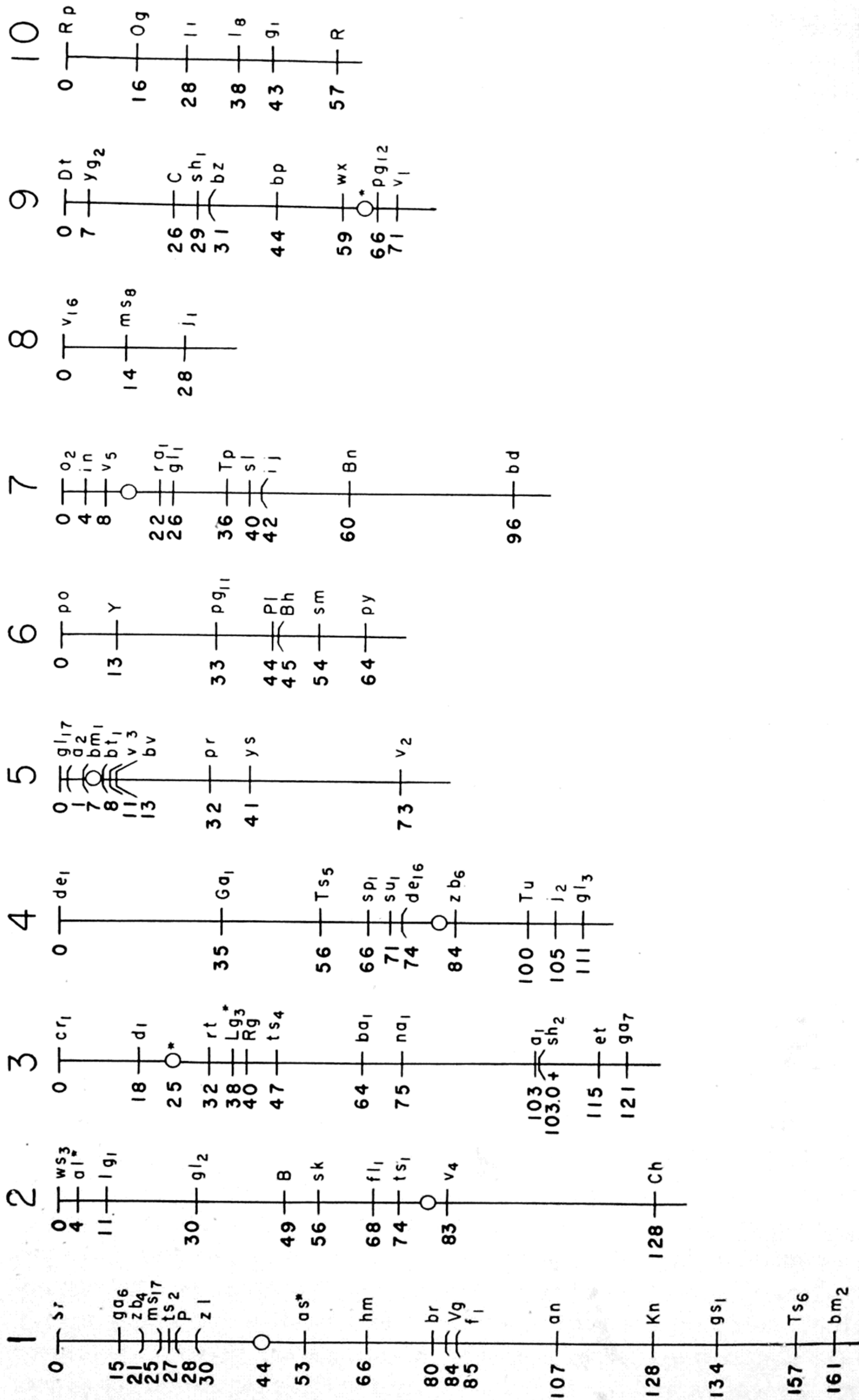


FIG. 7. Linkage maps of maize. The genes in linkage group 1 are carried by chromosome 1, etc. The zero ends of the maps are in the short arms of each chromosome. Centromeres are indicated by circles but only those whose location is known with some certainty are included. Asterisks indicate approximate locations.

were examined cytologically at meiosis to determine if a physical exchange of chromatin occurred between the two cytological markers when a genetic crossover within this region took place. Creighton and McClintock (1931, 1935) found that genetic crossovers in regions between the two heteromorphic points were invariably accompanied by an exchange of segments between the two chromosomes. For example, the gene yg_2 is close to the terminal knob, there being only a few per cent of crossing over between them, and C is 20 units distant from yg_2 . When a genetic crossover between yg_2 and C took place, they found that the terminal knob genetically close to yg_2 was transferred to the homologous chromosome coincidentally with a transfer of the yg_2 allele. This demonstration of the coincidence of genetic and cytological crossing over is an excellent example of how cytological studies can be used to confirm a genetically reasoned conclusion. Stern (1931) in his extensive study in *Drosophila* found a similar correlation. Brink and Cooper (1935), using a different cytogenetic setup from that employed by Creighton and McClintock, reported additional evidence of this correlation.

2. Relation between Crossing Over and Postdiplotene Association

Homologous chromosomes which are in intimate association at pachynema tend to repel each other and fall apart at diplonema. They are prevented from so doing by the presence of chiasmata. According to the chiasma theory of pairing it is the chiasmata which are responsible for the association of paired homologues from diplonema until anaphase I. The chiasma theory of pairing has been widely accepted, and many observations seem to support it. Although we may accept the general validity of this theory, even though it does not hold for *Drosophila* (Cooper, 1945), there is less agreement concerning the relationship between chiasmata and crossing over. According to the partial chiasmatype theory of crossing over, chiasmata are formed only when a crossover has occurred—i.e., the crossover occurs first and the chiasma appears when the paired homologues repel each other at diplonema. Prior to any movement of chiasmata along the chromosome arms, sister chromatids are associated on both sides of a chiasma (reductional plane). This theory requires a definite relationship between chiasma frequency and map distance. For regions where no double exchanges occur, the percentage of chiasmata should be twice the percentage of genetic recombination. The classical theory of crossing over postulates that chiasmata are formed by the opening out of the four chromatids in alternate reductional and equational planes; they do not represent points of prior crossing over. This theory demands no definite relationship

between chiasma frequency and map distance, since only those chiasmata which break at diplonema lead to genetic crossing over.

Beadle (1932a) in an ingenious experiment studied the relation between crossing over and chromosome association. Working with a translocation involving chromosomes 8 and 9 (T 8-9a) he determined the frequency of late prophase configurations in which a chiasma was apparently present in an interstitial region for which estimates of the percentage of recombination were available. The interstitial segment lying in the long arm of chromosome 9 between the centromere and the interchange point was associated, presumably by chiasmata, in 20 per cent of the pollen mother cells. Burnham (1930 and unpublished) had found 12 per cent recombination for this region. Since 10 per cent of recombination would be expected if every chiasma were a point of genetic crossing over, the agreement between observed and expected percentages seemed very good, and this experiment has been held to demonstrate the validity of the partial chiasmatype theory. Unfortunately, Beadle (1932a) did not obtain the recombination value for the interstitial region in those plants in which the chiasma frequency was cytologically determined. The great variability in crossover values found in different plants and in different strains argues against full acceptance of this correlation between chiasmata and crossing over. Moreover, a 2:1 relationship between chiasma frequency and map distance in interstitial regions would be found only if alternate and adjacent-1 segregations are equally likely to occur. Their relative frequencies are unknown.

3. Chromatid Crossing Over

There is convincing evidence that the exchange of segments occurs in the prophase stages of the first meiotic division when the two homologous chromosomes are in intimate association as a consequence of the synaptic attraction which is manifest at zygonema. The precise time at which crossing over takes place is a controversial matter, but it most likely occurs at early pachynema when reduplication of the chromonemata gives rise to two new chromatids. Prior to 1916 it was believed that crossing over took place before the paired chromosomes had divided equationally. On this basis each crossover would produce only crossover strands. Bridges (1916) concluded from his study of nondisjunction of the X chromosome of *Drosophila melanogaster* that each chromosome was split equationally into two chromatids at the time of crossing over. This conclusion was later confirmed by other investigators with *Drosophila*. Anderson (1925) and Bridges and Anderson (1925) demonstrated that not only were the chromosomes double

but that only two of the four chromatids exchanged segments at any one point. Since from each crossover or chiasma there are two crossover and two noncrossover chromatids, it follows that the frequency of points of crossing over is twice as great as the percentage of crossover chromatids or amount of recombination found in genetic data. That is, if genes *A* and *B* are 10 units apart on the genetic map, crossing over takes place between these two loci in 20 per cent of the meiocytes.

In maize as in *Drosophila*, it has been possible through genetic studies to demonstrate that the chromosomes are divided into chromatids at the time crossing over occurs. In addition to the genetic proof it has also been possible in maize to show that crossing over takes place between chromatids by direct cytological observations.

In diploid organisms where the four chromatids of the meiotic tetrad are normally distributed one to each member of the quartet of cells derived from the two meiotic divisions, and where it is impossible to identify the four gametes coming from a single meiocyte, it cannot be determined by genetic methods if crossing over occurs between chromatids. A test for chromatid crossing over is possible when a gamete receives more than one of the four chromatids. In those individuals which have one or more chromosomes in triplicate it is a regular event for certain spores to receive two homologous chromosomes instead of one as in disomic plants. These hyperploid individuals afforded a genetic setup which was used to demonstrate chromatid crossing over (Rhoades, 1933a). Plants trisomic for chromosome 5 were chosen because of the accuracy with which trisomic and disomic sibs could be distinguished and also for the reason that it was possible to mark several points with mutant genes. Plants trisomic for chromosome 5 with the constitution

$$\begin{array}{lll} Bm & Pr & V_2 \\ Bm & Pr & V_2 \\ bm & pr & v_2 \end{array}$$

were used as the female parent in crosses with recessive strains. Among the ensuing progenies 4.1 per cent of the trisomic plants were homozygous for v_2 , 1.2 per cent were homozygous for *pr*, and none was found homozygous for *bm*. These exceptional trisomes homozygous for v_2 or *pr* came from $n + 1$ eggs carrying the recessive allele in both of their chromosomes 5, although the recessive allele was present in only one of the three maternal chromosomes (Fig. 8). In many of the $n + 1$ eggs homozygous for v_2 one of the chromosomes carried the *bm* and *pr* alleles and was therefore a noncrossover chromosome while the other chromosome 5 had the *Bm* and *Pr* alleles and was a crossover. Similar combinations of crossover and noncrossover chromosomes were

found in the $n + 1$ eggs with two recessive *pr* alleles. These combinations could arise only from chromatid crossing over, with the exchanges involving only one of the two recessive chromatids.

The *bm* locus is in the short arm of chromosome 5 but lies so close to the centromere that crossing over rarely occurs between it and the centromere. The *pr* and v_2 loci lie in the long arm, with v_2 situated beyond the knob and *pr* lying between v_2 and the centromere. The linear order with the intervening crossover values for these three loci is *bm*-25 *pr* 41 v_2 . If there is no crossing over between a given locus and the centromere, there will be no trisomic individuals homozygous for the

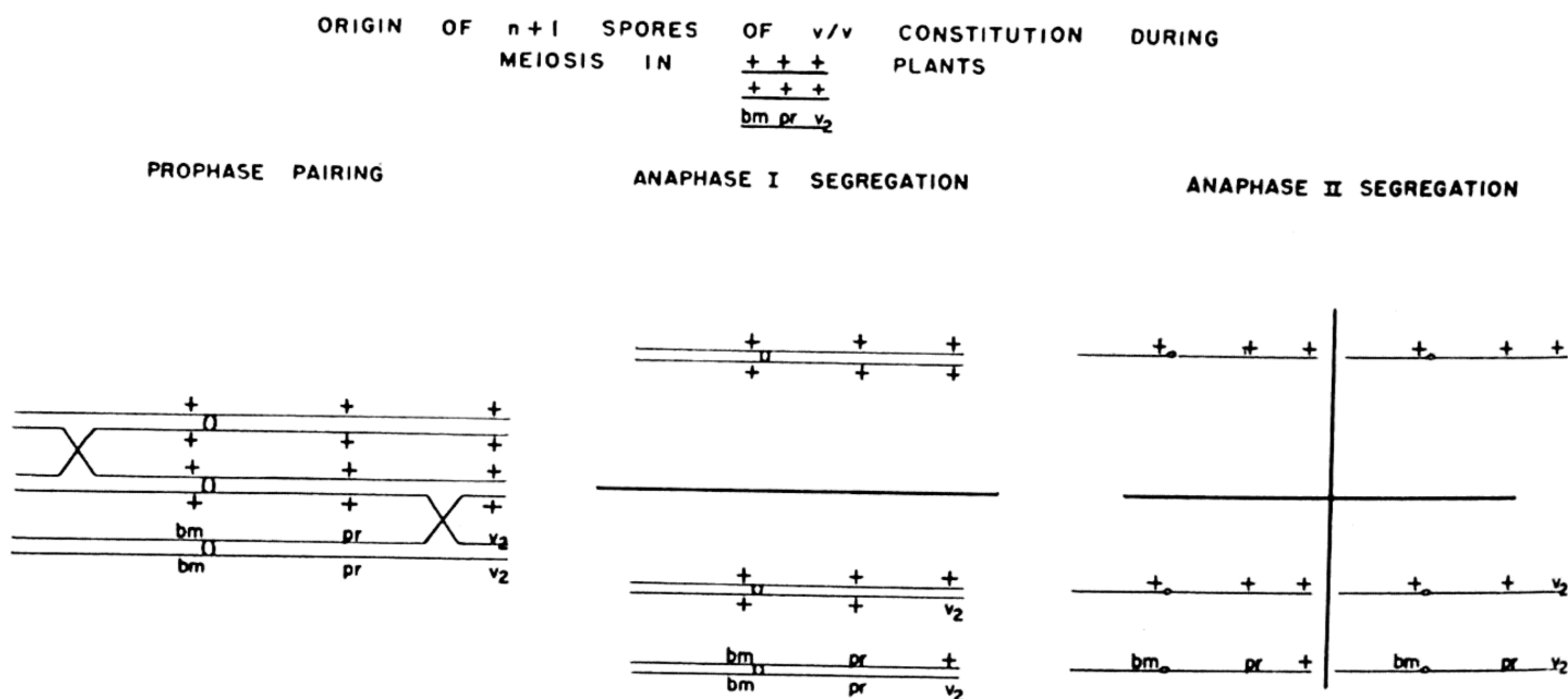


FIG. 8. Diagram of chromatid crossing over in trisomic plants. Only one kind of anaphase I disjunction is shown. The lower right combination, resulting from this anaphase I segregation, has two chromosomes 5 with the recessive v_2 allele but one is a crossover and the other a noncrossover. Combinations of this kind could arise only from crossing over between chromatids.

recessive allele of this locus; on the other hand, the more frequent the crossing over between a locus and the centromere, the more often recessive trisomic plants should appear. The observed frequencies of v_2 , *pr*, and *bm* trisomes are in agreement with their positions in chromosome 5.

Cytological proof of chromatid crossing over has been obtained with the use of structurally modified chromosomes where the crossover chromatids are made morphologically different from the noncrossover chromatids. This has been done with both translocations and inversions (McClintock, 1931, 1933, 1938a; Creighton and McClintock, 1932). The most direct and elegant of these demonstrations is the one involving the use of an inverted segment. Let the usual or normal gene order be represented as *A B C D E* and assume the centromere lies to the left of *A*.

If the *B C D* segment is inverted, i.e., rotated 180 degrees, the order becomes *A D C B E*. If pairing occurs between all homologous loci in individuals heterozygous for the inversion, a loop-shaped configuration is produced by the synapsis of those loci included within the inversion (see Fig. 9). If a crossover occurs in the inversion loop between undivided chromosomes, there would result one chromosome with two centromeres and one acentric fragment. The single dicentric chromosome would form a chromatin bridge at anaphase I because its two centromeres would pass to opposite poles while the acentric fragment would be released on the spindle. On the basis of chromosome crossing

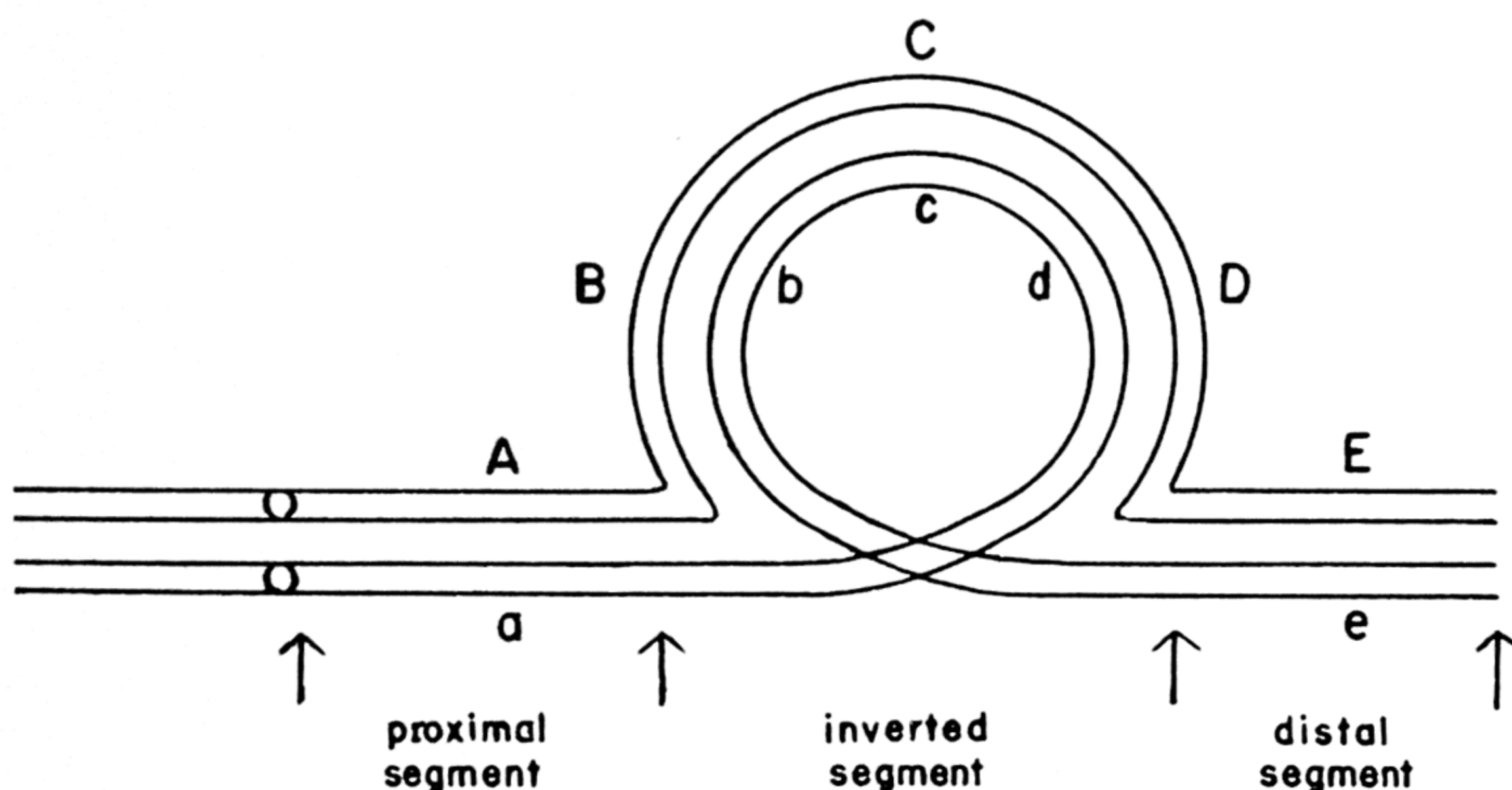


FIG. 9. Diagram of pairing in a heterozygous paracentric inversion. One chromosome has the *A B C D E* genes in a normal order while the other chromosome with the recessive alleles has the *b c d* segment in an inverted order.

over crossovers within the inverted region would yield only dicentric and acentric chromosomes. If, however, crossing over occurs between chromatids and only two of the four chromatids were involved, single exchanges within the inversion should result in a tetrad consisting of two centric noncrossover chromatids, one dicentric chromatid, and one acentric chromatid. The dicentric chromatid would form a chromatin bridge at anaphase I while the acentric chromatid lagged on the spindle, but the two noncrossover chromatids would pass to opposite poles (Fig. 10). McClintock, utilizing an inversion in chromosome 8 (1933) and one in chromosome 4 (1938a), showed that the result of single crossovers within the inversion loop was that expected with chromatid crossing over. McClintock (1938a) also found that a second crossover within the inversion involving the two chromatids not concerned in the first crossover (a four-strand double exchange) produced at anaphase I two dicentric chromosomes and two acentric fragments. The frequency

of cells with two bridges and two fragments was extremely low because of interference.

4. Chromatid Interference and the Upper Limit of Recombination

When two crossovers occur in a bivalent chromosome there are three possible kinds of double exchanges. Two-strand doubles are those in which the same two nonsister chromatids are concerned in both exchanges. In three-strand doubles one of the two strands involved in one exchange does not partake in the second crossover. In four-strand

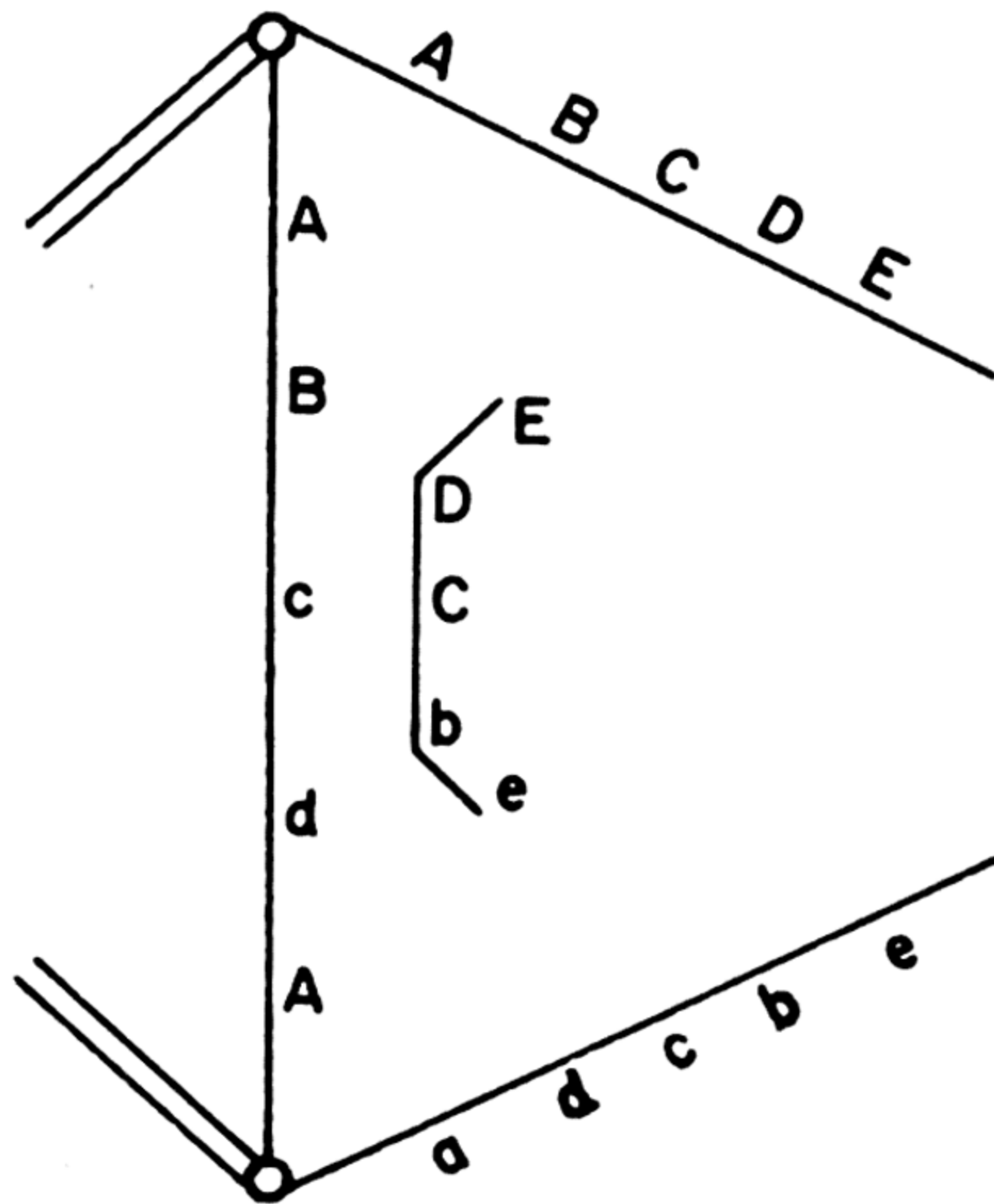


FIG. 10. Diagram of anaphase I configuration in a heterozygous paracentric inversion where one crossover has occurred in the inversion loop to produce a dicentric chromatid and an acentric fragment.

doubles the two chromatids involved in one exchange are the noncross-over chromatids at the second exchange. If it is wholly a matter of chance as to which two nonsister chromatids exchange segments at any point of crossing over—i.e., with random chromatid crossing over—then two-strand, three-strand, and four-strand doubles occur in a ratio of 1:2:1. Genetic studies by Beadle and Emerson (1935), Emerson and Beadle (1933), Sturtevant and Beadle (1936), and others indicate that in *Drosophila* there is random chromatid crossing over. Giles' (1934) cytological data in *Gasteria* also suggest the absence of chromatid interference, but it has been reported in *Neurospora*, *Trillium*, and *Stenobothrus*. Studies on a paracentric inversion (Rhoades and Dempsey, 1953) and unpublished data by Rhoades on the genotypic constitution

of diploid eggs resulting from nondisjunction at the second meiotic division in plants homozygous for the elongate gene both indicate that in maize there is no chromatid interference.

If in a given bivalent there is one exchange between two loci, 50 per cent of the chromatids will be crossovers and 50 per cent will be noncrossovers, since only two of the four chromatids are involved in the exchange of segments. Two-strand doubles between two loci yield two double crossover and two noncrossover chromatids. Three-strand doubles produce one noncrossover, two single-crossover, and one double-crossover chromatids, whereas in four-strand double exchanges all four chromatids are single crossovers. The resulting strands from all double exchanges are found in a ratio of 1 noncrossover: 2 single crossovers: 1 double crossover. Since the double-crossover chromatids have the two loci in the parental association, they are not recombinants as is true for the noncrossover strands. All of the single-crossover chromatids are recombinations, so the ratio of chromatids with parental combinations to new or recombinations is 1:1. A similar ratio is found when more than two exchanges occur, as is illustrated in the following table taken from Emerson and Rhoades (1933). It follows that the percentage of recombination between any two genes no matter how far apart they are on the linkage map can never exceed 50 with random chromatid crossing over.

TYPES OF RECOVERED CHROMATIDS

<i>Number of crossovers</i>	<i>0 Noncross- over strands</i>	<i>1 Single- crossover strands</i>	<i>2 Double- crossover strands</i>	<i>3 Triple- crossover strands</i>	<i>4 Quadruple- crossover strands</i>	<i>5 Quintuple- crossover strands</i>
1	16	16				
2	8	16	8			
3	4	12	12	4		
4	2	8	12	8	2	
5	1	5	10	10	5	1

That 50 per cent is the upper limit of recombination in maize is illustrated by the following data from Emerson and Rhoades (1933).

<i>Map distances</i>		<i>Recombination values</i>	
<i>P</i>	0	<i>P-as</i>	25
<i>as</i>	25	<i>P-f₁</i>	41
<i>f₁</i>	58	<i>P-an</i>	45
<i>an</i>	75	<i>P-bm₂</i>	49
<i>bm₂</i>	128		

Although P and bm_2 are 128 map units apart, they show approximately 50 per cent recombination. Many other examples could be cited in maize where 50 per cent is the upper limit of recombination irrespective of map distance.

The upper limit of 50 per cent for recombination values in maize is undoubtedly a consequence of random chromatid crossing over, but it should be recognized that the occurrence of this upper limit cannot be offered as proof of random chromatid crossing over. Indeed Jennings (1923) on the basis of chromosome crossing over pointed out that crossing over without interference or with interference extending not more than 30 units should give recombination values not exceeding 50 per cent.

5. Sister-Strand Crossing Over

Although McClintock (1938b) suggested that the production of double-sized dicentric rings from single-ring chromosomes could arise

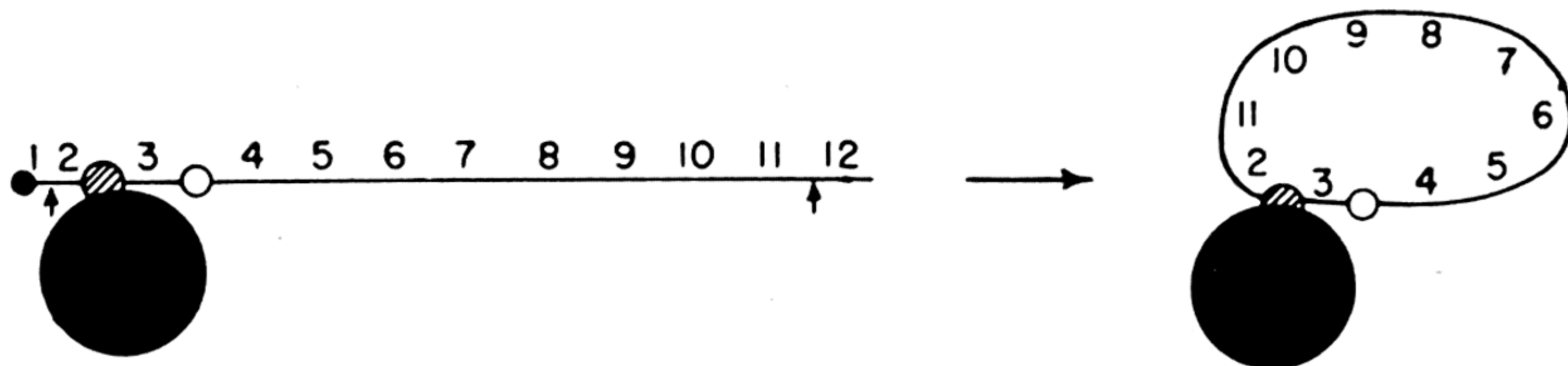


FIG. 11. Diagrammatic representation of the formation of a ring chromosome 6. The nucleolus is shown by a large black circle, the centromere by a clear circle and the nucleolar organizer by a circle with diagonal lines. The arrows indicate the breakage points (from Schwartz, 1953a).

from sister-strand crossing over in somatic cells, the evidence from studies with attached-X's, with the Bar locus, and with ring chromosomes in *Drosophila* was interpreted as proving that little or no meiotic crossing over occurred between sister strands. It should be emphasized that sister-strand crossing over cannot be detected in rod-shaped chromosomes, with the possible exception that unequal crossing over involving sister rod chromatids could give rise to duplicated and deficient segments. Recently, however, the important discovery by Schwartz (1953a, b) that sister-strand crossovers do occur forces us to reconsider all former concepts of the mechanism of crossing over and of chromosome reduplication. Schwartz studied the cytological consequences of crossing over in maize heterozygous for a normal chromosome 6 and for a ring-shaped chromosome 6 (1953c) which was deficient for part of the satellite region and for a small distal segment of the long arm

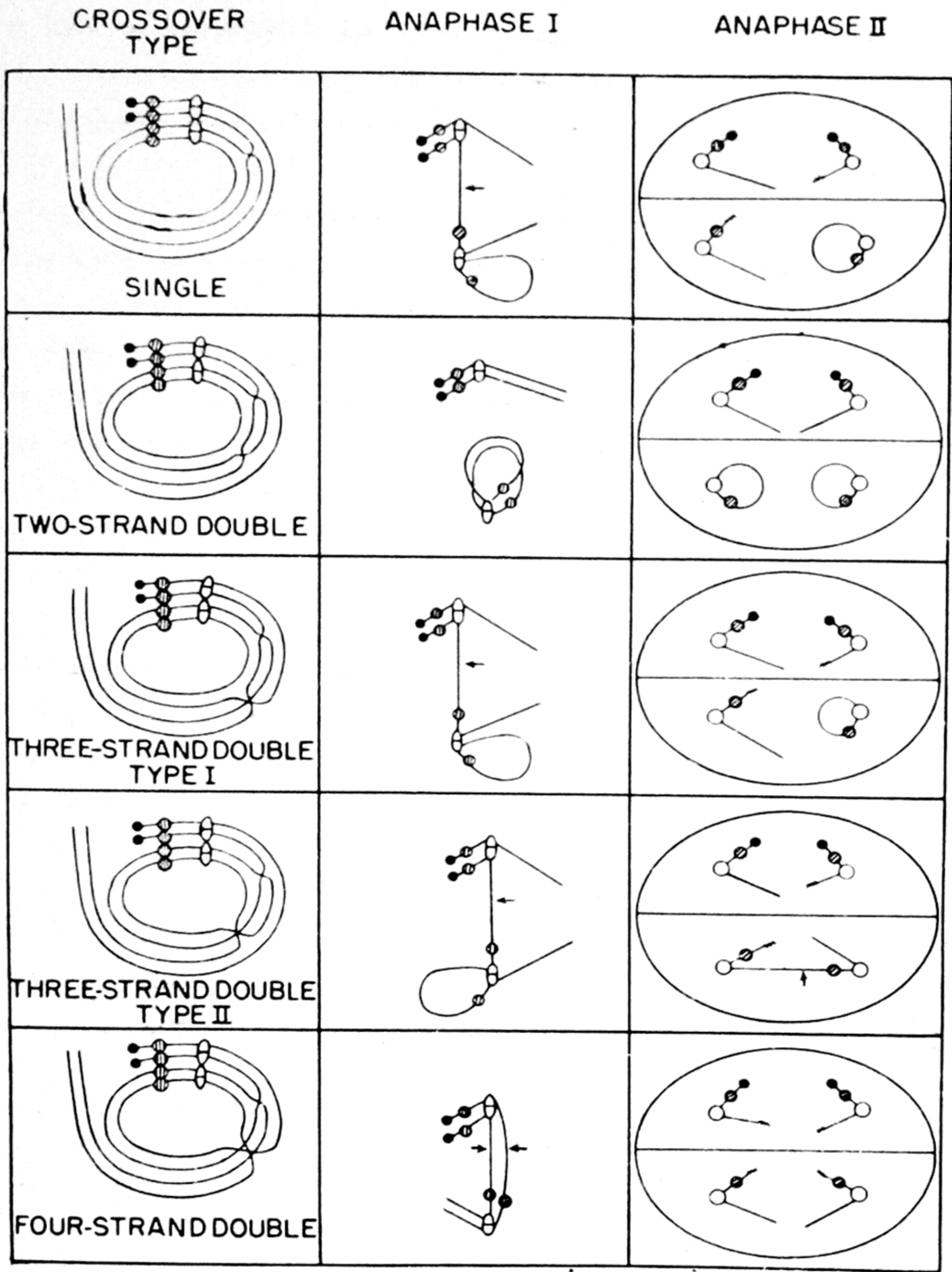


FIG. 12. Anaphase configurations resulting from different types of crossovers between a ring chromosome 6 and a normal rod chromosome 6 (from Schwartz, 1953a).

(Fig. 11). The types of configurations at anaphase I and anaphase II are illustrated in Fig. 12 and their frequencies are as follows:

Anaphase I					Anaphase II (daughter cell pairs)				
	Single bridge	Double bridge	No bridge	Total		Single bridge	Double bridge	No bridge	Total
No.	368	81	171	620		166	47	262	475
%	59	13	28	100		35	10	55	100

Only crossovers in the long arm between the ring and rod chromosomes 6 were considered. A single crossover involving two nonsister

chromatids gives rise to a single bridge at anaphase I and no bridge at anaphase II. No bridges at either anaphase arise from two-strand doubles. Type I three-strand doubles, where the same ring chromatid is involved in both crossovers, produce a single bridge at anaphase I and no bridge at anaphase II. A type II three-strand double with the same rod chromatid involved in both exchanges yields a single bridge at anaphase I and a single bridge at anaphase II. Four-strand doubles produce double bridges at anaphase I but no bridge at anaphase II. Two of the anaphase configurations can be assigned to certain types of double exchanges. The frequency of type II three-strand doubles can be determined from the percentage of single bridges at anaphase II, whereas double bridges at anaphase I come only from four-strand doubles. As the table shows, Schwartz found that 35 per cent of the anaphase II cell pairs had a single bridge, but only 13 per cent of double bridges were found at anaphase I. Equal numbers of these two kinds of configurations are expected if there is no chromatid interference. It was shown that negative chromatid interference could not account for the much higher frequency of apparent three-strand doubles. Furthermore he found that 10 per cent of the cell pairs at anaphase II had a double bridge in one of the cells. This is a class that is unexpected from either single or double exchanges. However, the high frequency of both single bridges at anaphase II and of the double bridges at anaphase II can be satisfactorily accounted for if crossing over occurs between sister strands.

The four classes of anaphase configurations which arise from double exchanges involving only nonsister strands are: single bridges at anaphase I only from type I three-strand doubles, single bridges at anaphase I and anaphase II from type II three-strand doubles, double bridges at anaphase I from four-strand doubles, and no bridges at either anaphase from two-strand doubles. These four kinds of double exchanges will be equally frequent if there is no chromatid interference and the available data indicate that this is true (see Section VI on chromatid crossing over). The proportions of these four classes will not be changed if sister-strand crossing over occurs, so the frequency of single bridges at anaphase II resulting from double nonsister exchanges associated with sister-strand crossing over should be equal to the frequency of anaphase I double bridges.

Single bridges at anaphase II can arise, in addition to those coming from type II three-strand doubles, from single exchanges between two nonsister chromatids which are associated with sister-strand crossing over in the ring chromosome. It is the anaphase II bridges from this source which are responsible for the high frequency of single anaphase

II bridges compared to that of double bridges at anaphase I. An odd number of sister-strand crossovers in the ring chromosome gives a single bridge at anaphase I and anaphase II, whereas an even number produces a single bridge at anaphase I only.

The unexpected class of double rings at anaphase II arises from sister-strand crossing over in the ring chromosome when there are either no nonsister exchanges or two-strand nonsister double exchanges.

The demonstration of sister-strand crossing over led Schwartz (1954) to propose a new theory for the mechanism of crossing over. Rejecting the torsion theory because it failed to explain why breaks produced by stress should occur in precisely the same place in two chromatids, he suggested that nonsister exchanges always involve the two newly formed chromatids. On this theory, which is a modification of that of Belling, only two-strand double exchanges occur. However, if sister-strand crossovers occur, and not necessarily at the same time as nonsister strand crossing over, some of the two-strand double exchanges are converted into three- and four-strand doubles. A two-strand double exchange is changed into a three-strand double if one, or an odd number of, sister-strand crossovers occurs in one of the chromosomes between the two nonsister exchanges. One, or an odd number of, sister-strand crossovers in each homologue in the same region converts the two-strand double to a four-strand double, whereas with no, or an even number of, sister-strand crossovers in both chromosomes the two-strand double remains unchanged. The evidence from the ring/rod heterozygotes indicated that the number of sister-strand crossovers was high per bivalent. If this is true there is an equal chance of an odd or even number occurring in each homologue between the two nonsister-strand exchanges and the ratio of 1 two-strand:2 three-strand:1 four-strand double exchange, which is expected on the basis of random chromatid crossing over involving only nonsister chromatids, would be found with sister-strand crossing over.

6. The Cytological Location of Genes

The physical location of gene loci along the pachytene chromosome is accomplished indirectly by combining cytological observations with genetic data. Several kinds of chromosomal aberrations, including deficiencies, duplications, inversions, and translocations, have been used effectively, but translocations have been most widely employed. The location of the point of interchange in the linkage map can be determined genetically, since it can be followed as if it were a dominant gene producing 50 per cent pollen and ovule abortion. Cytological examination at pachynema reveals the position of the break. If the break

point is between two linked genes, it is logical to conclude that their physical locations lie on either side of the cytologically determined point of interchange. As cytological and genetical data on other translocations involving the same region of the chromosome are obtained, it is possible to determine with ever-increasing precision the physical location of specific loci. Anderson and Longley (largely unpublished) have accumulated a vast amount of cytogenetical data on translocations which have made possible the approximate location of many genes in the pachytene chromosomes. The location of the centromeres rests in large part upon cytogenetical data from translocations (Anderson and Randolph, 1945). It should not be forgotten, however, that the reduction in crossing over in regions adjacent to the translocation point is often so great that the physical location of a gene locus may be lacking in the desired precision.

Theoretically, the physical location of genes can be more accurately determined with deficiencies, but in practice this is true only for terminal losses. McClintock (1944) obtained chromosomes 9 lacking extremely small portions of the end of the short arm. These were cytologically recognizable because of their terminal position. She was able to assign the *yg₂*, *pyd*, and *wd* loci to specific and minute portions of the chromosome. It would not be possible to see internal deficiencies of comparable size. Her placing of the *yg₂* locus in the terminal chromosome of the short arm is in agreement with Creighton's (1934) less exact determination that it is near the end of the short arm. Stadler and Roman (1948) obtained three X-ray induced changes at the *A₁* locus in the long arm of chromosome 3 which were proved by genetic tests to be minute internal deficiencies but which were not cytologically demonstrable. Larger, and less efficient, internal deficiencies are visible at pachynema in heterozygous plants. The pairing of a normal chromosome with one carrying an internal deficiency should produce a buckling of the normal chromosome opposite the deficient segment to compensate for the missing piece of the deficient chromosome. Unfortunately the buckles are not produced or are too small to be recognized with small deficiencies and in larger ones the position of the buckle is not constant but varies because of nonhomologous pairing.

The usual method of producing deficiencies which can be used to locate the physical positions of gene loci in the pachytene chromosome is by X-raying pollen with the normal allele and using it in crosses with plants homozygous for the recessive allele. A cytological study of the *F₁* individuals with the mutant phenotype discloses which of the treated paternal chromosomes has a deficient segment. There may be a different deficiency in each of the *F₁* plants, but all should have a segment

in common which represents the location of the missing normal allele. When a number of overlapping deficiencies are studied, even though all are fairly long and individually would permit only an approximate determination, the physical location of a specific gene can be delimited with accuracy.

A cytological study of induced deficiencies has been successful in locating a number of loci. The unplaced japonica gene was shown by McClintock (1933) to lie in the distal portion of the long arm of chromosome 8. The location of the gene for resistance to *Puccinia sorghi* (*Rp*) was first determined by deficiencies in the short arm of chromosome 10 (V. H. Rhoades, 1935). Stadler (1933) found that a deficiency for the distal one-sixth of the long arm of chromosome 10 included the *R* locus and (1935) that the v_3 gene was in a short proximal segment of the long arm of chromosome 5. McClintock (1931) located the *lg*₁ gene in the terminal four chromomeres of the short arm of chromosome 2. Inasmuch as ultraviolet irradiation produces more terminal deficiencies than do X-rays and since terminal losses are easier to recognize cytologically, the deficiencies induced by ultraviolet provide favorable material for the cytological location of gene loci. Singleton (1939) studied a number of terminal ultraviolet-induced deficiencies. The v_4 locus was found to lie in the proximal one-fifth of the long arm of chromosome 2 and the *A*₁ locus in the distal three-fifths of the long arm of chromosome 3.

The minute deficiencies produced by losses of segments from ring chromosomes, owing to their instability, have been used to associate certain loci with definite segments of the chromosome. McClintock (1941a) found a ring chromosome consisting of the proximal four chromomeres of the short arm of chromosome 5 which carried the *bm*₁ locus as well as three loci whose existence was unsuspected because no mutant alleles had been reported. A larger ring composed of the nine proximal chromomeres of the same arm possessed the same four loci as well as several others located in the five additional chromomeres.

Duplications have been used in locating genes cytologically. As is true for deficiencies, the smaller the duplicated piece which can be shown to carry certain genes the more accurate is the physical placement. Perhaps telocentric fragments are the most useful. Rhoades (1936a), studying plants hyperploid for a telocentric chromosome consisting of the entire short arm of chromosome 5, found that the *A*₂ and *bm*₁ loci are in the short arm, whereas the *bt*₁ locus, which is only one map unit to the right of *bm*₁, lies in the long arm. This permitted the relatively precise location of the centromere region, since it must be situated between these two closely linked loci. In the discussion on

translocation (Section VII) we mention how deficient-duplicate gametes and A-B translocations have been used in the placement of genes.

7. *Distribution of Crossovers in the Cytological Chromosomes*

In *Drosophila* a comparison of the cytological and genetical maps indicates that crossing over per unit of physical length near the centromere is less frequent than in distal regions. This reduction in crossover frequency has been attributed to the influence of the centromere, since it has been demonstrated (Beadle, 1932b) that an increase in recombination values occurs when a proximal segment is shifted away from the centromere. Conversely, regions normally near the distal ends undergo a reduction in crossing over when brought close to the centromere. There is some evidence in maize that crossing over in distal segments is much more frequent per unit of physical length than in more proximally located regions, but it has not yet been conclusively demonstrated that the difference is due to the centromere rather than to the heteropycnotic regions adjacent to the centromere.

Perhaps the most striking evidence of a disproportionate frequency of crossing over in distal regions comes from studies with the short arm of chromosome 9. According to McClintock (1944) this arm has about 20 chromomeres. The proximal one-third is characterized by large, deep-staining, closely packed chromomeres which have been likened to the heterochromatin of *Drosophila* chromosomes. The distal two-thirds of the short arm is said to be euchromatic because it is composed of small, widely spaced chromomeres. The total length of the genetic map of the short arm is between 60 and 70 units; the uncertainty is due to the difficulty of ascertaining the amount of recombination between the most proximal locus and the centromere. The *wx* locus lies approximately in the middle of the short arm of the pachytene chromosome. The amount of recombination between *wx* and the centromere, which is a segment comprising about one-half of the entire arm, is not more than 12 map units. The distal half of the short arm extending from the *wx* locus to that of *Dt*, which is in or near to the terminal knob, has a map length of 59 units (Rhoades, 1945). The γg_2 locus is situated in the terminal chromomere of the short arm (McClintock, 1944). Disregarding the heteropycnotic terminal knob, the only part of the short arm distal to γg_2 is the threadlike strand which connects the ultimate chromomere and the knob. Although physically very near one another the *Dt* and γg_2 loci are 7 map units apart.

A striking demonstration of a progressive increase in crossing over in more distal regions comes from McClintock's (1943) studies of chromosomes 9 deficient in varying extents for terminal portions of

the short arm. The deficiencies ranged in size from the loss of the terminal chromomere to loss of four chromomeres. The *C* locus is within the fifth or sixth chromomere from the end of the short arm. The amount of crossing over between *C* and the end of the deficient chromosome could be determined in plants heterozygous for the different deficiencies. The following recombination values were found for the various deficiencies:

<i>Extent of deficiency</i>	<i>Per cent of crossing over between C and end of deficient chromosome</i>
4 chromomeres	1.00
3 chromomeres	1.25
2 chromomeres	3.07
1½ chromomeres	8.33
1 chromomere	17.06
1 chromomere	21.00

An increase in length of only half a chromomere increased the cross-over units by 10. It is clear that a disproportionate amount of crossing over occurs in the distal segments of the short arm of chromosome 9.

Evidence for the unequal distribution of crossovers along the chromosomes also comes from studies with chromosomes 5 and 2. Morgan (1950) found that in In2b one break point was in the middle of the short arm of chromosome 2. The map length of the short arm is about 79 crossover units. The distal half of the short arm has 66 of these units, whereas the proximal half is only 13 map units long. McClintock (1938b, 1941a) obtained a chromosome 5 deficient for the proximal one-third of the short arm. The deficient segment did not include the *A*₂ locus, which is only 6 crossover units from the centromere. Since the short arm of 5 has an estimated map length of over 70 units, the distal two-thirds has approximately 11 times as much crossing over as the proximal one-third.

McClintock's (unpublished) data on crossing over in interstitial segments of heterozygous translocations involving the short arm of chromosome 6 (see Section VI, 9, "Variability in Crossing Over") also indicate that crossing over is increased in segments more distant from the centromere. The frequency of crossing over in the longer interstitial segment of the 5-6 translocation was disproportionately higher than in the short interstitial segment of the 6-10 translocation.

8. *Estimates of Total Lengths of Genetic Maps of Maize Chromosomes*

Although maize has been the subject of intensive cytogenetical studies, most of the observations have been confined to the critical pachytene stage, and very little attention has been given to the series

of stages between pachynema and diakinesis which are collectively known as diplonema. It is at this stage that chiasmata first are in evidence, and any investigation which purports to establish a relationship between chiasma frequency and crossover distance should place considerable emphasis upon the number of chiasmata found at diplonema as well as at later stages. Darlington (1934) made an attempt to determine the total chiasma number for all the chromosomes in maize and to translate this number into crossover units which he prorated among the 10 chromosomes on the basis of their pachytene length in order to arrive at an estimate of the total map distance of each chromosome. The task would have been much simpler if it were possible to recognize each bivalent chromosome at diplonema and to determine for each the mean chiasma frequency which, assuming that every chiasma is equal to 50 per cent crossing over, could readily be converted to crossover units representing the total length of the genetic map. If the chromosomes were populated with mutant genes throughout their entire lengths so that the total map distance could be determined, it would then be possible to compare the length for each chromosome computed from the mean chiasma number with the length determined from crossing-over data. If a good agreement were found between the calculated and observed map distances, it would be good evidence of the correctness of the chiasmatype theory of crossing over. It was to obtain such proof that Darlington (1934) was lead to study chiasma frequency at diplonema and the later stages of diakinesis and metaphase. Unfortunately, however, the individual chromosomes cannot be recognized at diplonema or diakinesis (except for chromosome 6, which is attached to the nucleolus) so Darlington counted the total number of chiasmata present in all of the chromosomes. He found an average of 2.7 chiasmata for the 10 bivalents at diplonema. The chiasma frequency was reduced slightly to 2.5 at diakinesis, presumably by the fusion of 2 chiasmata in one arm as they moved to the end or terminalized. If the total of 27 chiasmata were allotted among the 10 chromosomes on the basis of their pachytene length, the longest chromosome would have 3.9 chiasmata and the shortest would have 1.7. An average chiasma value of 1.7 for chromosome 10 would mean that in at least 30 per cent of the cells this bivalent would have a single chiasma. Darlington (1934) observed that the frequency of bivalents with a single chiasma was only 2.2 per cent; thus he assumed that a nonlinear relationship existed among the 10 chromosomes with regard to chiasma frequency and pachytene length, i.e., the shorter chromosomes have more chiasmata per unit of length than do the longer members of the complement. On the basis of this nonlinear relationship he assigned to each of the 10 bivalents its share

of the total of 27 chiasmata and from these hypothetical chiasmata frequencies he calculated the total length of each chromosome in terms of crossover units. His results are given in the following table with the known lengths of the genetic maps as determined from the best available data.

<i>Number of chromosome</i>	<i>Relative pachytene length</i>	<i>Chiasma frequency</i>	<i>Map length in crossover units</i>	
			<i>Calc.</i>	<i>Obs.</i>
1	100	3.65	187	161
2	86	3.25	163	128
3	78	3.00	150	121
4	76	2.95	148	111
5	76	2.95	148	73
6	53	2.20	110	64
7	61	2.45	123	96
8	61	2.45	123	28
9	53	2.20	110	71
10	44	1.95	98	57

This table shows that in no case does the observed length exceed the calculated, and in many it is considerably less. Approximately 500 mutant genes are known in maize, but only a fraction of these have been assigned a definite place in the genetic maps. The lengths of the maps will be considerably extended as more unplaced genes are located. It is obvious that the total length of any chromosome cannot be ascertained unless its two distal ends are marked by mutant genes or by some visible morphological characteristic which can be used as a marker. Admittedly it will be difficult to determine the total map length from linkage studies involving only mutant loci because there is no way of estimating the amount of undetected crossing over occurring beyond the most distally placed locus. By the employment of a terminal knob it is possible to obtain the crossover percentage between the end of the chromosome arm and some mutant locus occupying a more proximal position and, if this procedure is possible for the other arm, to arrive at the total map length of the chromosome. Although there are several terminal knobs available in the different chromosomes which could be thus used, this has been done only for the short arm of chromosome 9.

9. Variability in Crossing Over

When the amount of crossing over in a given region is determined for different plants or in the two sexes of individual plants, a consider-

able amount of variability is found among the crossover percentages. It is possible to ascertain by appropriate statistical methods if the observed variability can be wholly accounted for by errors of sampling or if some real difference exists in crossover frequency. Studies of variations in crossing over in chromosome 9 have been made by Stadler (1926) and Collins and Kempton (1927). These studies were facilitated by the use of three linked genes which affect the endosperm. These genes are *C c* for aleurone color, *Sh sh* for endosperm development, and *Wx wx* for the type of starch molecule. Since the endosperm arises from the fusion of a sperm with the two polar nuclei, each kernel, as far as the endosperm characters are concerned, represents an individual and a single ear comprises a progeny of several hundred. It is possible, therefore, to obtain large numbers of individuals with relatively little effort.

Stadler, who studied chiefly variability among sister plants of a single family, found that crossing over in the first and second ears of the same plant was highly correlated, whereas Collins and Kempton found a negative correlation among the plants of one progeny but in another found a positive correlation. Stadler (1926) reported that crossing over in the male and female gametes of the same plant was not significantly correlated, i.e., there was no pronounced tendency for crossing over to be high among the male gametes if it was high among the female. Collins and Kempton (1927) reported in one progeny a negative correlation and in another a significant positive correlation. Both Stadler and Collins and Kempton concluded that crossing-over percentages from several samples of one individual were less variable than samples from different individuals of the same family. They were in agreement that there was no significant increase or decrease in crossing over with age. According to Stadler crossover variations among the male gametes were possibly negatively correlated with date of first pollen shedding, and variations in the female gametes were correlated negatively with plant height, number of ears, and perhaps with number of tillers. The cause of these possible correlations remains wholly unknown.

Collins and Kempton (1927) stated that crossing over between *C* and *Wx* was slightly but significantly less when the *R* locus in chromosome 10 was in a heterozygous condition. Significant differences were found between the mean crossover values in different families. They reported that one strain gave with some consistency 35 to 39 per cent of recombination for *C* and *Wx* and that another had from 17 to 22 per cent. They also reported that crossing over varied from 8 to 50 per cent among individuals of different progenies. Stadler (1926) in a

single comparison of two plants from unrelated families found wide and significant differences in crossing over.

Stadler (1926) concluded that crossing over among individuals of one family in the *C-Sh*, *Sh-Wx*, and *C-Wx* regions in either sex was only moderately variable if allowance was made for errors of sampling. Collins and Kempton (1927) reached a similar conclusion for some progenies, but in others the variability between sister plants was so large they concluded that factors other than chance were affecting the crossover mechanism. Although the nature of the disturbing factors which Collins and Kempton believed responsible for the great variability in crossing over in their material was never resolved, cytogenetic investigations by other workers have disclosed a number of situations in which chromosome synapsis and consequently crossing over are disturbed.

Pertinent data related to variability in genetic crossing over were obtained by McClintock (unpublished) on the frequency of exchanges within the interstitial segments of translocation heterozygotes involving the short arm of chromosome 6. Tetrads in which exchanges had occurred within this region gave rise to quartets of microspores which could be cytologically distinguished from quartets derived from non-crossover tetrads (see Section VII, "Translocations" for details of this technique). Using a translocation between chromosomes 6 and 5 with a long interstitial segment, she found that the frequency of exchanges within this region was nearly the same in all anthers of a single plant from which one collection of sporocytes had been made but that there were marked variations in the percentage of crossover quartets from plant to plant, ranging from 45 to 75 per cent. In plants with a translocation involving chromosomes 6 and 10, which had a short interstitial segment approximately one-half the length of that in the 6-5 translocation, the frequency of exchanges was likewise uniform in single collections of anthers from each plant, but there was a range from 3 to 14 per cent in different plants. Her data deal with the frequencies of no exchange and exchange tetrads rather than with the percentage of crossover chromatids, but they can be converted to recombination percentages by halving the exchange frequencies.

10. Crossing Over in Male and Female Flowers

Crossing over in maize occurs during micro- and mega-sporogenesis. A number of maize students, notably Emerson and Hutchison (1921), Eyster (1921, 1922), Stadler (1926), and Collins and Kempton (1927) have determined the relative frequency of crossing over in the two sexes.

Emerson and Hutchison (1921) found a significantly higher percentage of crossing over for the *C-Sh* region of chromosome 9 in the female gametes of certain plants, but other data by these investigators and also by Eyster show no significant differences in crossing over for this region in the two kinds of flowers. Stadler (1926) found significantly higher crossover values for the *C-Sh*, *Sh-Wx*, and *C-Wx* regions in the male gametes. Collins and Kempton (1927) reported a higher rate of crossing over for the *C-Wx* region in the male gametes of four progenies, but in nine progenies the female gametes had higher percentages of crossing over. In six of the nine progenies with higher crossing over in the female gametes the differences are clearly significant, and in three of the four progenies where the male gametes had higher recombination percentages the differences are also significant. Eyster (1921, 1922) found no significant differences between the two sexes in recombination value for the *Su-Tu* region of chromosome 4. Emerson and Hutchison (1921) reported a similar conclusion for the *lg-B* region of chromosome 2. Rhoades and Rhoades (1939) found no marked differences in crossing over between the male and female gametes for three regions of chromosome 10.

The discordant results found by different investigators for the same region, the failure to find any difference in several regions, and the fact that where a difference was observed between the two sexes it was of such small magnitude that large numbers of individuals were necessary to establish its statistical significance, all suggested that there was no consistent variation in crossing over associated with sex in maize. This generalization has been accepted by maize students, and usually no attempt has been made to indicate which parent was heterozygous when crossover values from backcrosses were reported. That this practice is not always justified is indicated by the data of Rhoades (1941a), who found that crossing over in the *A₂-Bt*, *A₂-Bm*, *Bt-Pr*, and *Bm-Pr* regions of chromosome 5 was significantly higher in the male flowers than in the female. Since these four regions were adjacent to the centromere, it was suggested that differences in crossing over in male and female flowers might be confined to regions near the centromeres. In agreement with this idea is the fact that those regions for which no consistent differences were found lie some distance removed from the centromere. Unpublished data by Burnham on crossing over in proximal regions of several chromosomes also show higher recombination values in male than in female flowers. The cause of this sexual difference remains obscure. In addition to the various explanations advanced by Rhoades (1941a) there is the further and more likely possibility that selective orientation of the tetrad on the meiotic spindles could lead to the

noncrossover chromatids being preferentially segregated to the basal megaspore. If this were true, crossing over could be equally frequent in both kinds of flowers, but the observed amount would be less in the female gametes.

When the amount of recombination in male and female gametes is determined for two loci, one affecting an endosperm and the other a sporophytic character, there is the possibility that the male value will be higher because of heterofertilization. Sprague (1932a) found that occasionally sperm from two pollen tubes were involved in the fertilization of a single ovule. A sperm from one pollen tube united with the egg while a sperm cell from a second tube fused with the polar nuclei to form the endosperm. These two sperm cells could be dissimilar genetically when a heterozygous individual was used as the pollen parent and would lead to unlike genetic constitutions of the embryo and endosperm. The extent of heterofertilization varied greatly in different lines, but it is a factor which must be taken into consideration before concluding that a real difference exists in crossover frequencies in male and female flowers.

VII. Translocations

The first translocations found in maize were of spontaneous origin. Brink (1927) and Brink and Burnham (1929) suggested that the genetic behavior of their case of "semi-sterility" could be satisfactorily accounted for by assuming a translocation between two nonhomologous chromosomes, but it was not until Burnham (1930) found the expected rings of four at diakinesis and McClintock (1930) observed the intimate synaptic relationships of a translocation complex at pachynema that the hypothesis was firmly established. Following these pioneer studies a number of papers appeared dealing not only with the cytogenetical behavior of other translocations but more importantly with their employment as cytogenetical tools in the elucidation of related problems such as the correlation of cytological with genetical crossing over, the relationship between the percentages of chiasmata and genetic recombination, and the placement of certain genes in specific regions.

Although the first translocations arose without treatment, the great majority of those which have been studied have been induced by ionizing radiation. In a recent paper Longley (1950) lists 588 different translocations whose points of interchange have been cytologically determined, and nearly all of these were induced. Anderson and his associates at Pasadena are making an extensive study of these induced translocations, and most of the recent work on translocations comes from this laboratory.

Translocations are reciprocal exchanges of segments between non-homologous chromosomes. Simple translocations, where a fragment of one chromosome becomes terminally attached to an unbroken end of another chromosome, have never been found in maize or in any other organism. Translocations arise when breaks occur in two different chromosomes, thus producing four chromosome fragments each with a broken end. Restitution of broken ends restores the original condition and no structural change is produced. If the broken end of one centric fragment unites with the broken end of the second centric fragment, a dicentric chromosome is formed. Dicentric chromosomes are unstable because a chromatin bridge arises at anaphase when the two centromeres are directed to opposite poles. This dicentric bridge either is broken by tension at anaphase or is ruptured by cell plate formation at telophase. If not eliminated from either pole, its genic constitution is constantly subject to change. The acentric chromosome resulting from the union of the two acentric fragments forms no chromosomal spindle fibers at mitosis and hence is lost because of its irregular anaphase movement. Following breaks in two chromosomes the union of broken ends is often such that dicentric and acentric chromosomes are formed, but they are not transmissible.

If, however, the broken end of the centric fragment of one chromosome unites with the broken end of the acentric fragment of the other chromosome and the acentric fragment of the first becomes attached to the centric fragment of the second chromosome, two interchanged monocentric chromosomes are formed, each with a block of genes from the two parental nonhomologous chromosomes. These interchanged chromosomes behave normally throughout the somatic mitoses and are completely stable. In plants homozygous for the interchange there are two new pairs of chromosomes whose behavior is in no way different from that of the other eight pairs. Depending upon the location of the points of interchange, the new chromosomes may or may not have a different morphology and length. Since the interchanged chromosomes are composed of segments from two nonhomologous chromosomes, those loci in the interchanged segments near the break points will show close linkage, although in structurally normal plants they would be independently inherited. In plants heterozygous for two normal and two interchanged chromosomes a four-armed synaptic configuration is produced at pachynema by the pairing of homologous regions (Fig. 13A).

Cytologically the points of interchange in the two chromosomes can be determined by studying the synaptic configurations at pachynema in plants heterozygous for the translocation. The center of the cross

configuration would denote the break points if strictly homologous pairing occurred. Unfortunately, the nonhomologous association frequently found in translocation figures makes it difficult to ascertain the exact points of interchange, unless, as is sometimes the case, the break points occurred in regions of strikingly dissimilar chromomere pattern.

The points of interchange determine the lengths of the four arms of the quadripartite figure at pachynema. Two opposite arms of the cross have centromeres, but the other two are without centromeres. The two segments between the centromeres and the center of the cross are known as interstitial regions. If the two points of interchange were close to the centromeres, crossovers would infrequently occur in the interstitial regions. Translocations of this type form open rings of four at diakinesis (Fig. 13C), since there will be one or more crossovers in each of the four arms. However, if an additional crossover occurs in an interstitial region a figure-8 complex results at diakinesis. The frequency of these figure-8 complexes is determined by the number of crossovers in the interstitial segments; it will be high in those translocations where one or both of the break points are some distance removed from the centromere. One of the four arms of the cross configuration will be short in those translocations where the break in one chromosome is near the end. There may be a failure of synapsis of the two homologous regions comprising the short arm or there may be no crossing over if pairing is achieved. Chains (Fig. 13D) rather than rings of four characterize translocations of this type (Burnham, 1932a). When the interchange points in both chromosomes are nearly terminal two "pairs" rather than chains or rings of four are found because of the lack of pairing and consequently of crossing over in both short arms of the translocation complex (Clarke and Anderson, 1935).

The open ring of four of diakinesis moves onto the MI spindle, where it assumes either a zigzag arrangement or remains as an open ring. The zigzag orientation (Fig. 13F) leads to alternate chromosomes of the ring passing to the same pole at anaphase. If, for example, we have a translocation involving chromosomes 2 and 5 with one break near the centromere in 2L and one in 5S also close to the centromere, the ring of four will consist of two normal chromosomes, 2 and 5, and two interchanged chromosomes, 2^5 and 5^2 . The 2^5 chromosome has a centromere from chromosome 2, while the 5^2 chromosome obtained its centromere from chromosome 5. With alternate disjunction the normal 2 and 5 chromosomes go together and the two interchanged chromosomes 2^5 and 5^2 pass to the opposite pole at anaphase I. The quartet of spores formed at the end of the two meiotic divisions will consist of two microspores with normal chromosomes and two with the interchanged

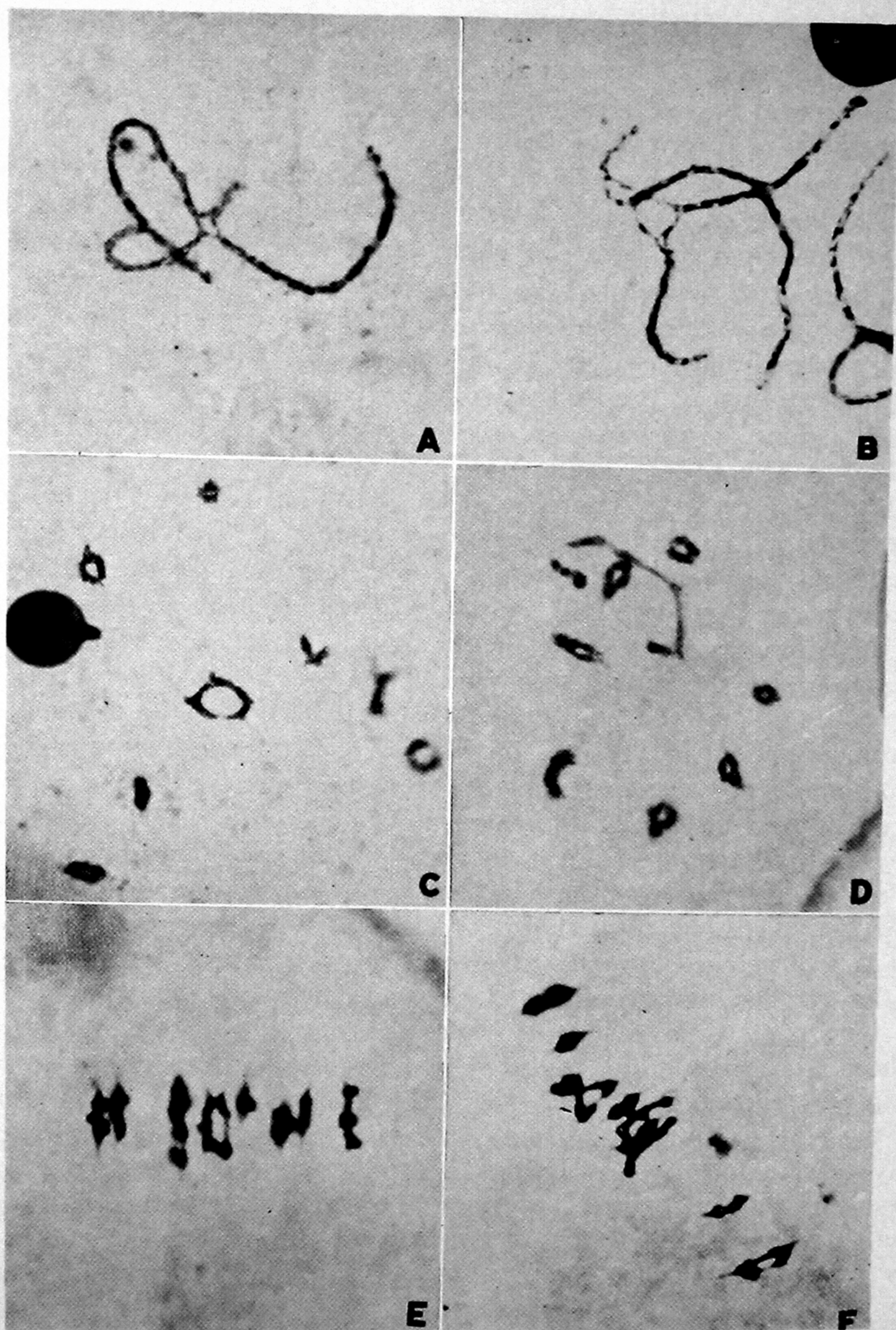


FIG. 13. Photomicrographs from translocation heterozygotes. Propionic carmine smear preparations.

A. Pachytene pairing in translocation between chromosomes 8 and 10. The center of the cross denotes the points of interchange.

B. Pachytene pairing in translocation between chromosomes 4 and 9. The short

chromosomes. All four will develop into functional male gametophytes, since none is deficient or duplicate for any genes.

However, instead of the ring of four assuming the zigzag orientation on the spindle it may become attached to the spindle as an open ring (Fig. 13E). This will result in adjacent members of the ring passing to the same pole. In adjacent-1 segregation homologous centromeres pass to opposite poles, i.e., chromosome 2 disjoins with 5^5 while 5 goes with 2^5 . All four spores of the resulting quartet will be deficient and duplicate; consequently they will abort. With adjacent-2 disjunction, homologous centromeres pass to the same pole. In the above example this would mean that chromosome 2 went with 2^5 and 5 with 5^2 . As in the case of adjacent-1 segregation all four microspores would abort because of their deficient-duplicate constitution.

If alternate and the two kinds of adjacent segregation occurred at random, two-thirds of the pollen would be abortive. However, since approximately 50 per cent of the pollen is viable, the number of pollen mother cells with an alternate orientation is equal to the sum of those with the two types of adjacent segregation. Ovule sterility is also about 50 per cent, indicating that orientation of the ring of four is essentially the same in megasporocytes as in microsporocytes. In translocations similar to the one described above where all four arms are long while the interstitial segments are short, the proportion of alternate:adjacent-1:adjacent-2 segregations is 2:1:1. When chains of four occur at diakinesis, there will be a ratio of 1 alternate to 1 adjacent orientation at metaphase I but only adjacent-1 segregations occur. In those translocations not involving chromosome 6 it is difficult to determine the ratio of the two kinds of adjacent segregation and to assess the effect of interstitial crossovers on disjunction.

The use of chromosome 6 with its nucleolar organizer has made it possible to determine the kinds of segregation in translocation heterozygotes which involve the short arm of this chromosome. This is owing to the fact that certain kinds of segregation lead to recognizably different

arm of 9 (near nucleolus) terminates in a small knob. The centromeres of 4 and 9 are in close association and appear to be fused.

C. Ring of four at diakinesis. Rings of four are produced when one or more chiasmata are present in each of the four arms of the translocation configuration.

D. Chain of four at diakinesis resulting from a failure of chiasma formation in one of the four arms of the translocation configuration.

E. Orientation of the ring of four on the metaphase I spindle leading to adjacent segregation of the members of the ring.

F. A zigzag orientation of the ring of four at metaphase I which produces an alternate segregation of the members of the ring.

quartets of microspores in terms of number of nucleoli present (see Figs. 14 and 15). Burnham (1949, 1950), following the earlier work of McClintock (1934, 1945), made an extensive study of translocations involving chromosome 6. Burnham reached the following conclusions regarding chromosome segregation and crossing over in the interstitial regions. (1) In those translocations with no crossing over in the interstitial regions, adjacent-1 and adjacent-2 segregations occur with approximately the same frequency (*ca.* 25 per cent each). Both lead to the production of abortive deficient-duplicate spores. Alternate segregation which produces viable spores took place in 50 per cent of the microsporocytes. (2) There is no adjacent-2 segregation following crossing

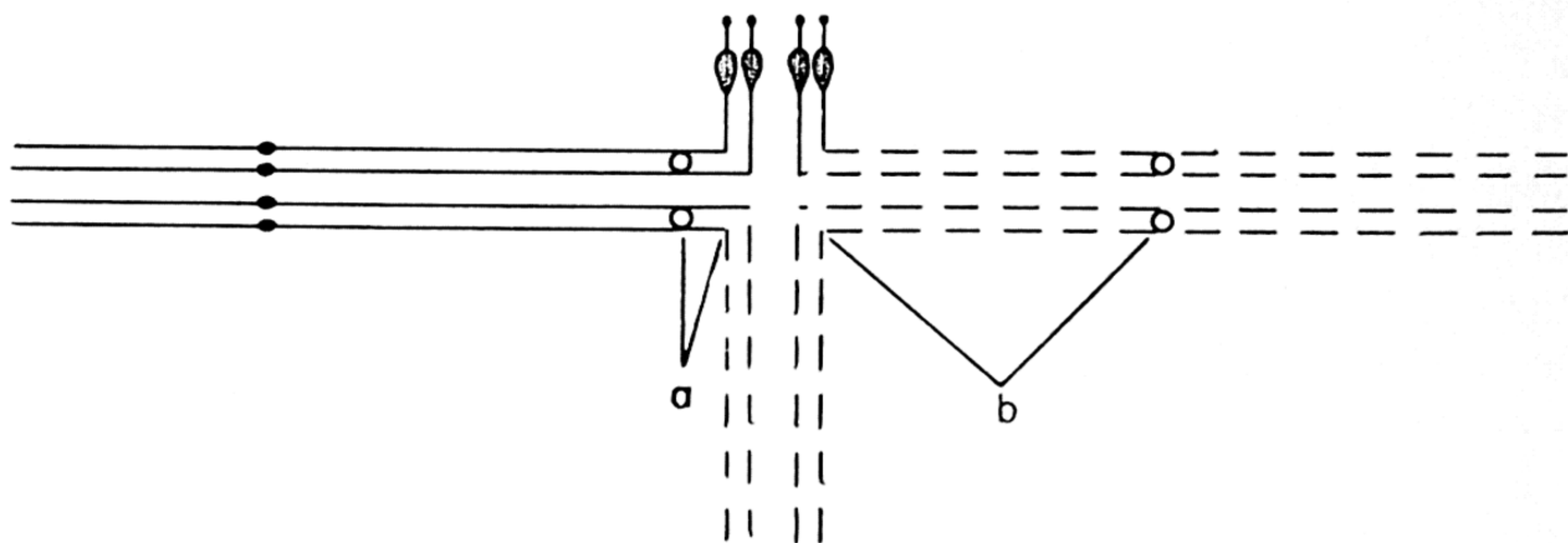


FIG. 14. Pachytene configuration of translocation heterozygote involving chromosomes 5 and 6. The break in chromosome 6 is in the short arm near the centromere, and the break in 5 is in the long arm. Since the interstitial segment (*a*) lying between the centromere of 6 and the translocation point is very short, crossing over in this interval would occur infrequently, but the other interstitial segment (*b*) between the translocation point and the centromere of 5 is long enough to permit frequent crossover (after Burnham, 1950).

over in the interstitial regions. In those translocations having long interstitial segments with frequent crossovers there was little if any adjacent-2 segregation, but in translocations with very short interstitial regions adjacent-2 segregations were as frequent as adjacent-1. It was not possible to distinguish cytologically between alternate and adjacent-1 segregation when interstitial crossovers occurred. Both types produce quartets with two viable and two abortive spores. (3) Chain-forming translocations had low frequencies of adjacent-2 segregation irrespective of the amount of crossing over in the interstitial segments.

The relationship between chiasma formation and the amount of genetic recombination within an interstitial segment depends upon the relative frequencies of alternate and adjacent-1 segregation. Following a single exchange within the interstitial region, two of the four chromatids are crossovers and two are noncrossover chromatids. If alternate

segregation occurs, the two crossover chromatids are included in the abortive spores and the two noncrossovers are in the viable spores. The reverse distribution is found with adjacent-1 segregation, since the two viable spores have the crossover chromatids and the two lethal spores the noncrossover strands. It follows that the observed amount of genetic recombination within the interstitial segment will be influenced by the kinds of segregation which occur. This may be illustrated as follows. Assume 20 per cent of the microsporocytes have one

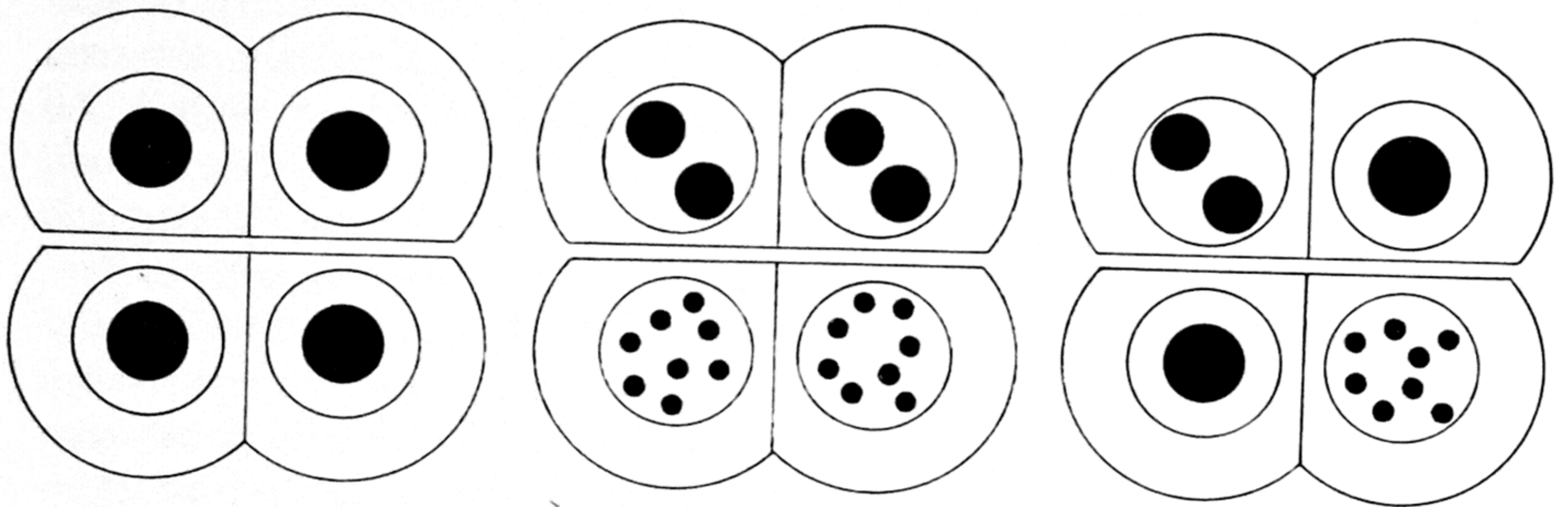


FIG. 15. The principal types of microspore quartets found in plants heterozygous for translocations involving the short arm of chromosome 6. The spore quartet to the left, where each spore has one nucleolar-organizer region and hence one nucleolus, comes from alternate and from adjacent-2 segregations when the break in chromosome 6 is in the short arm. If the interchange point is in the long arm of 6, both alternate and adjacent-1 segregations give this type of quartet. The center quartet, where two spores have two nucleoli each since they possess two organizers and where the other two spores have the nucleolar material dispersed among many droplets (diffuse type) owing to the lack of an organizer, comes from adjacent-1 segregation if the break in 6 is in the short arm and from adjacent-2 segregation if the break is in the long arm. The rightmost quartet, where one spore has two nucleoli, two have one nucleolus, and one spore has no organizer and is of the diffuse type, is found in translocations with the break in the short arm of 6 when there is a crossover in an interstitial region followed by either alternate or adjacent-1 segregation (after Burnham, 1950).

chiasma (equals genetic crossing over) in an interstitial region which is marked by mutant genes. No adjacent-2 segregation occurs following these interstitial crossovers. If the ratio of alternate to adjacent-1 segregation is 1:1, the per cent of genetic recombination will be 10 per cent or one-half the chiasma frequency, as is normally the case. However, if only alternate segregation takes place, no recombination will be found, and 20 per cent recombination will be realized if only adjacent-1 segregation is possible. A ratio of 3 adjacent-1:1 alternate segregation would give a recombination value of 15 per cent. It follows that any attempt to relate the percentage of genetic recombination to the frequency of cytologically observed chiasmata in an interstitial region

will lead to equivocal results as long as the relative frequencies of segregation types remain unknown.

Studies of translocations between B chromosomes and members of the basic set (A chromosomes) by Roman (1947) have led to a number of interesting findings. Randolph (1941) found that the great majority of the offspring from the cross of 0 B female by 2 B male had 0 B or 2 B chromosomes, with only a few carrying the 1 B chromosome. The reciprocal cross consisted chiefly of individuals with 1 B chromosome as expected, since in the 2 B parent the 2 B chromosomes usually formed a bivalent. That normal disjunction of this B bivalent usually occurred is evidenced by the fact that in 130 microspores Randolph found 116 with 1 B and only 14 with none. Since no microspore was found with more than 1 B chromosome, the high frequency of the unexpected 2 B class of offspring suggested to Randolph that the B chromosome underwent mitotic nondisjunction during the formation of the male gametophyte or pollen grain. If nondisjunction occurred at the first microspore division, the two sperm cells formed by the division of the generative nucleus would have either 0 B or 2 B chromosomes, depending upon whether the tube or generative nucleus received the 2 B chromosomes. In either event the two sperm cells in a pollen grain would be identical. However, if nondisjunction occurred at the second rather than at the first microspore division, the two sperm cells would be dissimilar, since one would have 0 B and the other would possess 2 B chromosomes. It is not technically feasible to determine the behavior of B chromosomes during gametogenesis by direct cytological observation nor is it possible to use genetic methods, since the B chromosome is devoid of active chromatin and has no phenotypic effect. Roman (1947) was able to elucidate the behavior of pieces of the B chromosomes by involving them in translocations with A chromosomes and using the mutant genes provided by the latter as genetic markers for the B chromatin.

His translocation T B-4a, involving chromosome 4 and a B chromosome, is particularly instructive. The point of interchange in chromosome 4 is in the short arm approximately one-eighth of the distance from the centromere to the end of the arm. The break point in the B is at or near the junction of the euchromatic and the large heterochromatic segments (see Fig. 2). As a result of the exchange of segments two new chromosomes were formed. The 4^B chromosome has the distal acentric portion of the B attached to the centric fragment of chromosome 4, and the B^4 chromosome has a B centromere and the proximal portion of the B, to which is attached the acentric piece of the short arm of chromosome 4. The *Su* locus is in the piece of the short arm of 4 which was transferred to the B^4 chromosome. When plants homozygous

for the interchanged chromosomes, with the *Su* allele in both B^4 chromosomes, were used as the female parent in crosses with recessive *su* pollen parents, all of the resulting kernels were *Su* in phenotype. The reciprocal cross, however, gave ears with many kernels showing the *su* phenotype. These *su* kernels had no B^4 chromosome in the endosperm, but the embryos of such kernels carried two B^4 chromosomes. Likewise many of the *Su* kernels had hypoploid embryos lacking the B^4 chromosome, which presumably was present in duplicate in the endosperm. This dissimilarity in constitution of the embryo and endosperm shows that nondisjunction of the B^4 chromosome occurred at the second microspore division. Mitotic nondisjunction did not occur in 100 per cent of the microspores, since some of the embryos in *Su* kernels had one B^4 chromosome.

It is the B^4 and not the 4^B chromosome which undergoes mitotic nondisjunction. Apparently the centromere or the adjacent chromatin is responsible for nondisjunction. In Roman's different A-B translocations the B was broken at various places along its length, but it was always the interchanged chromosome with the B centromere which underwent nondisjunction. Roman (1949) found, however, that the B^4 chromosome underwent nondisjunction rarely, if at all, in microspores lacking the 4^B chromosome which possesses the heterochromatic segment derived from the B chromosome. This suggests that although the 4^B chromosome itself does not undergo nondisjunction, the presence of B heterochromatin in the nucleus is a necessary prerequisite for nondisjunction of the B^4 chromosome. The essentiality of B heterochromatin for nondisjunction of the B centromere could be established from the breeding behavior of the C, D, E, and F fragments of Randolph (1941), arising by fragmentation of the B chromosome, where different segments of B heterochromatin have been lost; but this has not yet been done. Both the genetic and cytological evidence indicate that nondisjunction occurs only in the development of the male gametophyte. Roman (1948a) reported that the class of kernels with hyperploid embryo and deficient endosperm was more frequent than the class with hypoploid embryo and hyperploid endosperm. Inasmuch as these two classes would be expected with equal frequencies, barring viability differences, if it were a matter of chance which of the two dissimilar sperms united with the egg and which with the polar nuclei, the disproportionate number of kernels with hyperploid embryos and deficient endosperm indicated that preferential fertilization occurred. The sperm cell with two B^4 and one 4^B chromosomes fertilized the egg more often than it united with the two polar nuclei. The converse was true for the hypoploid sister sperm with no B^4 and one 4^B chromosome.

According to Roman (1948b) preferential fertilization also occurs when one sperm of a pollen grain has two intact B chromosomes and the other has none as the result of nondisjunction at the second microspore division. The sperm nucleus with two B chromosomes fertilized the egg nucleus more often than did the no-B sperm. It was suggested that this could account for the persistence of B chromosomes in natural populations, since other factors such as their elimination through irregular meiotic behavior tend to reduce their numbers.

The A-B translocations promise to be extremely valuable genetic tools. They will be useful in studies of gene dosage, since they afford a means of obtaining individuals hypoploid for specific chromosomal regions as well as those redundant in varying degrees for these segments. Perhaps their greatest usefulness will be in placing unlinked genes. The locating of new mutants in one of the 10 linkage groups by conventional means is so expensive and unrewarding a task that few now undertake so tedious a program. However, crosses of plants homozygous or heterozygous for unplaced recessive genes by pollen parents with different A-B translocations carrying the normal alleles will disclose in the F_1 generation whether or not the new mutant is located in that piece of a specific A chromosome which undergoes nondisjunction by virtue of its being part of a chromosome with a B centromere. The mutant phenotype will be expressed in the hypoploid F_1 plants if the locus of the tested mutant is in the missing segment of the A chromosome. In order to exploit fully this ingenious method of locating unplaced genes, 20 different A-B translocations are needed—two for each chromosome with the points of interchange close to the centromere and in different arms. The 11 A-B translocations which have been isolated are listed below with the points of interchange in the A chromosomes. The distance from the translocation point to the centromere is given as a decimal fraction of the total length of the arm. The long arms are designated by the letter "L" and the short arms by "S."

	<i>Position of break</i>
T B-1a	L 0.2
T B-1b	S 0.05
T B-3a	L 0.1
T B-4a	S 0.25
T B-6a	S 0.5 (in nucleolus organizer)
T B-7a	L 0.95
T B-7b	L 0.3
T B-8a	L 0.7
T B-9a	L 0.4
T B-9b	S 0.4
T B-10a	L 0.35

Although only approximately 30 per cent of the total chromatin of the 10 chromosomes is included in these A-B translocations, the coverage can be considerably extended by using hypoploid F_1 plants, even though the tested locus is not in the deficient segment. In their studies with the T B-1a translocation Roman and Ullstrup (1951) found that the gene for resistance to *Helminthosporium carbonum* (*Hm*) was located in the piece of 1L attached to the B centromere. As expected the hypoploid F_1 plants from crosses of *hm hm* plants with T B-1b pollen were all resistant. These resistant hypoploid plants carried the recessive *hm* allele in a normal chromosome 1 and the dominant allele for resistance in the 1^B chromosome. Although the break in T B-1b is in the short arm, it is very close to the centromere, with the result that all crossovers which transfer the *Hm* allele from the 1^B chromosome to a normal chromosome 1 occur in the long arm between the centromere and *Hm*. The only functional pollen produced by these hypoploid plants is that with a normal chromosome 1. Therefore the percentage of resistant plants in the progeny from the cross of a susceptible female parent by a resistant hypoploid F_1 individual is a measure of the amount of recombination between the *Hm* locus and the centromere. This proved to be 21.8 per cent. Obviously genes in the long arm further removed from the centromere would have less distorted ratios.

Laughnan and Coe (1953) have suggested a third use for these translocations as a way of screening for newly arising mutants in specific chromosome regions. Plants with A-B translocations are used as the pollen parent in crosses with *normal* plants. In the hypoploid F_1 plants and endosperms any mutation which has occurred in the corresponding segment of the normal chromosome will be expressed, since it will be hemizygous. Each F_1 hypoploid plant or endosperm tests a single gamete of the normal plant for mutation of all of the loci lying within this segment.

Certain reciprocal translocations involving only the A chromosomes may also be used to test for the location of unplaced genes. In those translocations where one break is near the end of one of the chromosomes, adjacent-1 disjunction yields spores deficient for the segment distal to the break and duplicate for a portion of the other chromosome. If the deficient segment is not too long or carries genes not essential for gametophyte development, these deficient-duplicate spores can develop into functional female gametophytes. When the egg of such a deficient-duplicate megagametophyte is fertilized by a sperm cell carrying a recessive allele, the F_1 individual will manifest the recessive character if this locus lies in the deficient segment. Patterson (1952) has used a number of different translocations producing functional deficient-duplicate

megaspores and has succeeded in placing several loci on the cytological maps of chromosomes 2 and 9. However, the utilization of this technique appears somewhat limited, since spores with large deficiencies abort and only relatively small regions can be tested in a hemizygous condition.

With the exceptions noted above functional spores come from alternate segregations which produce spores with the two normal chromosomes and those with the two interchanged chromosomes in equal numbers. When a plant heterozygous for the translocation is crossed with a structurally normal plant, two kinds of zygotes are produced: those homozygous normal and those heterozygous for the translocation. The homozygous normal plants have no pollen or ovule sterility, whereas individuals heterozygous for the interchanged chromosomes have 50 per cent aborted pollen and ovules. Since the occurrence of aborted pollen and ovules marks the presence of the interchanged chromosomes, the inheritance of the translocation may be followed in linkage studies as if it were a dominant gene for pollen and ovule abortion. The center of the pachytene cross configuration represents the points of interchange and is designated by the symbol T. Genes lying in the four arms of the cross will be linked with T and with each other, the intensity of the linkage being inversely proportional to the frequency of crossing over between T and the marker genes in each of the four arms. When only the recombination values between T and the loci of a single arm are considered, the usual linear map is obtained, with T located at one end of the map. However, T occupies a terminal position on the maps of each of the four arms and when recombination values between genes in all four arms are determined, the combined linkage data do not give a linear order but form a cross-shaped map with T at the center of the cross.

Recombination values for regions adjacent to the translocation point are usually lower in translocation heterozygotes than in normal plants. Cytological studies of synapsis at pachynema in translocation complexes have afforded an adequate explanation of this reduction in crossing over. In many pachytene figures it was observed that homologous regions were loosely paired at the translocation points. Since an intimate association of homologous regions is a necessary prerequisite for crossing over, the loose pairing often found near translocation points should result in a decrease in crossing over in regions adjacent to the breakage points. Pairing and consequently crossing over is nearly normal in those segments distantly removed from the translocation points. Burnham (1932b, 1934) and McClintock (1933, 1934) have shown that the

position of the center of the cross is not constant. Any shifting of the position of the cross from the true position involves the pairing of nonhomologous regions. Crossing over rarely occurs between nonhomologous regions, even when they are intimately paired; thus the occurrence of a considerable amount of nonhomologous synapsis should also decrease the frequency of crossing over. Burnham (1932b, 1934) observed more nonhomologous pairing and lack of pairing near the translocation points in some reciprocal translocations than in others and found that in those translocations where a greater disturbance of normal pairing occurred, there was a correspondingly greater decrease in crossing over in regions adjacent to the translocation points than in those translocations where pairing was more normal. Studies with other translocations have shown decreases in crossover frequencies which are undoubtedly caused either by the failure of pairing near the center of the cross or by nonhomologous association or both.

Translocations offer a number of advantages over mutant genes as genetic markers in studying the inheritance and linkage relations of genes determining agronomic characters. Among these are: (1) regions of chromosomes devoid of mutant genes can be marked by translocations; (2) the presence of the interchanged chromosomes has no effect on the morphology of the plant; and (3) the reduction in crossing over in regions adjacent to the translocation point results in a more effective linkage test.

Their use has led to a number of interesting findings. Freeman (1946), using translocation stocks in studies of the inheritance of husk length, ear length, and days-to-silking, found genes for long husks in chromosomes 1, 2, and 8 in inbred Florida 1 and in chromosome 1, 2, and 3 in inbred Florida 2. There were genes for ear length in chromosomes 1, 3, 4, 5, and 8 in inbred Florida 1, whereas inbred Florida 2 had such genes in chromosomes 4, 5, and 9. Genes for maturity, as indicated by days-to-silking, were found in chromosomes 3, 5, and 8 in Florida 1 and in Florida 2, which also had similar genes in chromosomes 1 and 2. Burnham and Cartledge (1939) and Saboe and Hayes (1941) found that several of the chromosomes carried genes determining smut resistance. Mann (1950) reported linkages between genes for row number and translocations.

Some of the most significant studies using translocations as cytogenetical tools were made with the earlier translocations of spontaneous origin. Included among these are the correlation of cytological and genetical crossing over and the relation between chiasmata and crossing over. These have already been discussed.

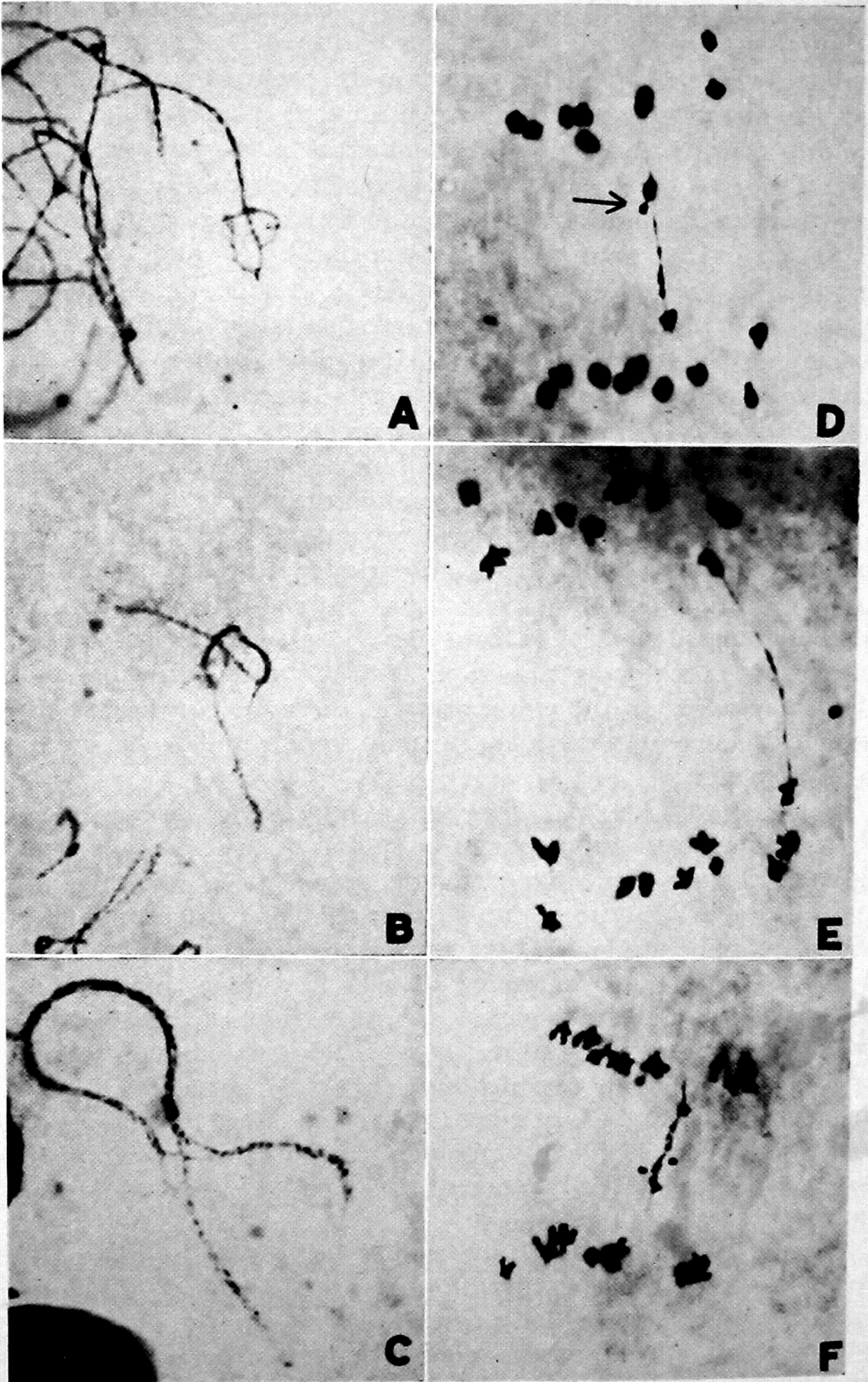


FIG. 16. Photomicrographs from inversion heterozygotes. Propionic carmine smear preparations. (See p. 183 for legend.)

VIII. Inversions

Compared with translocations little work has been done with inversions in maize, even though they constitute one of the more interesting types of aberrations. Convincing genetic evidence of inversions in *Drosophila* had been found by Sturtevant (1931). Their presence was indicated by the suppression of crossing over in heterozygous inversions where only double-crossover and no single-crossover chromosomes were recovered. Sturtevant demonstrated that flies homozygous for the inverted segments had a new linear order and normal crossing over. The first cytogenetical studies of inversions were made by McClintock (1931, 1933) working with maize. Later investigations of inversions in maize were reported by McClintock (1938a, 1939), Anderson (1936), Clark (1942), O'Mara (1942), Morgan (1950), Russell and Burnham (1950), and Rhoades and Dempsey (1953).

There are two kinds of simple inversions. In the paracentric type the inverted segment lies within a single arm of the chromosome, whereas in the pericentric type the centromere is included within the inverted segment. McClintock (1931, 1933) showed that in both types a loop-shaped configuration is produced at pachynema by the synapsis of the relatively inverted homologous regions (Figs. 16A, B, and C). However, the subsequent cytological behavior of the two types is strikingly different, since the dicentric bridges and acentric fragments produced by crossing over in heterozygous paracentric inversions are not found in pericentric inversions.

A typical paracentric inversion at pachynema is diagrammed in Fig. 9. The proximal region is that segment between the centromere and the beginning of the loop; the inversion loop consists of the inverted segment, and the distal portion is the terminal uninverted region. Listed below in Table I are the anaphase configurations coming from various types of exchanges.

A, B, and C are at pachynema and show the loop-shaped configurations produced by synapsis of relatively inverted segments. A is from a paracentric inversion in the long arm of chromosome 3 (In3a), and B and C are two different photographs of pericentric inversion 2a. Photo C is by Dr. D. T. Morgan, Jr.

D. Anaphase I from In3a with a single dicentric bridge where the acentric fragment, indicated by arrow, is associated with the end of a normal chromatid.

E. Anaphase I from In3a with a single dicentric bridge and a free acentric fragment.

F. Anaphase I from In3a with two dicentric chromatids and two acentric fragments produced by a four-strand double crossover within the inversion loop.

TABLE I

THE DIFFERENT KINDS OF ANAPHASE I AND ANAPHASE II CONFIGURATIONS FOUND IN PLANTS HETEROZYGOUS FOR A PARACENTRIC INVERSION

The four microspores arising from each pollen mother cell may be viable or abortive; if viable they carry either a noncrossover or a double-crossover chromatid. The constitution of the basal megaspore is given for each type of tetrad. Its constitution is uncertain following single and some double exchanges unless there is always selective elimination from the basal megaspore of the deficient chromatids derived from breakage of the bridge. This is true for some inversions but not for others.

		Microspores of quartets			Basal megaspores		
		Viable non- cross- over	Viable double cross- over	Abor- tive	Viable non- cross- over	Viable double cross- over	Abor- tive
Type of tetrad							
<i>Anaphase I</i> <i>configuration</i>							
1. No bridge No frag.	a. No exchange	4	0	0	1	0	0
	b. 2-strand double in loop	2	2	0	1/2	1/2	0
2. 1 bridge 1 free frag.	a. Single exchange	2	0	2	1?	0	?
	b. 3-strand double in loop	1	1	2	1/2?	1/2?	?
	c. 2- and 4-strand doubles with one exchange in loop and second in proximal region	2	0	2	1?	0	?
3. 1 bridge 1 attached frag.	a. 3-strand double with one in loop and one in distal region	2	0	2	1?	0	?
4. No bridge 1 frag.	a. 3-strand double with one in loop and one in proximal region	2	0	2	1/2	0	1/2
5. 2 bridges 2 frags.	a. 4-strand double in loop	0	0	4	0	0	1
<i>Anaphase II</i> <i>configuration</i>							
1. No bridge	a. From all of above types except No. 4						
2. 1 bridge	a. From No. 4 above						
3. 2 bridges (one in each sister cell)	a. Certain types of triple exchanges where two are in loop						

The frequencies of the different kinds of anaphase configurations at the first and second meiotic anaphases found by Rhoades and Dempsey (1953) for a paracentric inversion (In3a) in the long arm of chromosome 3 are as follows:

<i>Anaphase I</i>					<i>Anaphase II</i>	
No bridge No frag.	1 bridge 1 free frag.	1 bridge 1 attached frag.	No bridge 1 frag.	2 bridges 2 frags.	(single cell counts)	
					No bridge	1 bridge
925	577	37	87	19	458	17
(56.2%)	(35.1%)	(2.2%)	(5.3%)	(1.2%)	(93.2% P.M.C.)	(6.8% P.M.C.)

Dyads disjoin normally (i.e., no bridges or fragments are produced) when there has been no exchange or a two-strand double exchange within the inversion loop. A single exchange within the loop produces a tetrad with two noncrossover, one dicentric, and one acentric chromatid. Since anaphase I is reductional for the centromere region, a chromatin bridge is formed by the dicentric chromatid as its two centric regions pass to opposite poles (Fig. 16E). Cells with a single bridge and fragment also come from three-strand doubles within the loop and from two- and four-strand doubles where one exchange has taken place in the proximal region and a second within the loop. In some of the microsporocytes there is a single dicentric bridge, but the acentric fragment is found terminally attached with the end of the long arm of a normal chromatid (Fig. 16D). These attached fragments arise when there has been a single exchange within the loop and also one in the distal univerted region. If the distal region is short as is true for In3a, concomitant crossing over in the distal segment and in the loop will infrequently occur, so this class is small. An acentric fragment at anaphase I unaccompanied by a dicentric bridge is found following three-strand double exchanges where one crossover is in the inversion loop and the second is in the proximal region. One of the freely disjoining dyads is a dicentric loop chromatid which will form a bridge at anaphase II when the equational division of the centromere takes place. The frequency of anaphase II sister cells with a bridge in one cell should be equal to the number of anaphase I cells with one fragment and no bridge. The observed values for these two kinds of anaphase figures agree very well. Two bridges and two acentric fragments at anaphase I result from four-strand double exchanges within the inversion loop (Fig. 16F). The four-strand double exchanges are the only ones of the three kinds of double exchanges which are cytologically recognizable.

In maize as in *Drosophila* a great reduction in the observed amount of crossing over is found for loci located in the inverted segment. They are inherited as a block of closely linked genes. The only exceptions to complete linkage come from the relatively rare two- and three-strand double exchanges within the inversion loop which produce double-crossover chromatids. When no crossing over occurs, two of the four microspores arising from such microsporocytes will have a structurally normal chromosome and two will possess the inverted chromosome. All four spores, which carry noncrossover chromosomes, will develop into functional male gametophytes, since all have a full gene complement. Dicentric bridges and acentric fragments come from crossing over within the loop. The dicentric bridge is deficient for the distal segment, whereas the acentric fragment has this region in duplicate and also has the inverted segment of chromatin. The breakage of the dicentric bridge at the end of the first meiotic division produces two chromatids, both of which are deficient for the distal segment and which are deficient for, or carry in duplicate, portions of the chromatin comprising the bridge, depending upon the point of rupture. Spores possessing these deficient chromatids will abort. When a single exchange takes place within the inversion, the two crossover chromatids form the dicentric bridge and acentric fragment. The other two chromatids are noncrossovers. The two spores receiving the noncrossover chromosomes develop into functional pollen, but the two crossover chromatids are in the abortive spores and are not transmissible. Two-strand double exchanges produce two noncrossover chromatids and two double-crossover chromatids. All of the resulting four spores develop into viable gametophytes. Of the two functional spores with double-crossover chromatids one will have the normal and one the inverted order. Three-strand double exchanges give a single bridge and fragment which are cytologically indistinguishable from those produced by single exchanges but which differ genetically. Only two of the four chromatids are transmissible. One of these is a noncrossover while the other is a double-crossover chromosome. Two dicentric bridges and two acentric fragments arise from four-strand double exchanges. None of the four microspores coming from such pollen mother cells will function because of the deficient nature of the chromatids. The deficient microspores appear as empty collapsed grains which are vastly different from normal pollen. It is clear from the above that the percentage of aborted pollen reflects the amount and kinds of crossing over within the inversion loop. Although the frequency of exchanges may be high, genetic recombination is effectively suppressed, since functional crossover chromatids come from the comparatively infrequent two- and three-strand double

exchanges. In the inversion studied by Rhoades and Dempsey (1953) the inverted region was 61 map units long, but in crosses using inversion heterozygotes as the pollen parent only 1.1 per cent of the recovered chromosomes were crossovers. All resulted from double exchanges. In the reciprocal cross, double crossovers composed 1.8 per cent of the recovered chromosomes.

The combined cytological and genetical data on crossing over obtained by Rhoades and Dempsey (1953) permit a test for chromatid interference. On the assumption of no chromatid interference the expected number of double-crossover strands in the backcross progenies was 1.5 per cent when the pollen parent was the heterozygote and 1.9 per cent when the egg parent was heterozygous. These calculated values agree well with the observed values of 1.1 and 1.8 per cent, respectively, and indicate the absence of chromatid interference in maize. This conclusion is supported by unpublished data on the genotypic constitution of unreduced eggs produced by plants homozygous for the *el* gene (Rhoades, unpublished).

Realization of the role of the centromere in the anaphase movements of chromosomes came from the behavior of acentric fragments produced by inversion crossing over. The failure of these fragments to form chromosomal fibers at metaphase and their irregular movement on the spindle during anaphase, which led to their failure to be included in either telophase nucleus, demonstrated the essentiality of the centromere for orderly disjunction during mitosis.

McClintock (1938a, 1939, 1941b) showed that fusion of half-chromatids following breakage of a dicentric bridge at either meiotic anaphase resulted in formation of a dicentric bridge at the first gametophyte division. This bridge again breaks at anaphase, followed by fusion of the newly broken ends when the chromosome reduplicates, with the result that a dicentric bridge occurs at the next anaphase. This bridge-breakage-fusion cycle is found in the two mitoses of the male gametophyte and in the three mitoses of the female gametophyte. In Fig. 17, which diagrams the constitution of the dicentric bridge for In3a, the small distal segment 11 is not present in the bridge. If the bridge breaks between segments 2 and 3, as indicated in Fig. 17, one of the broken chromatids possesses the proximal segments 1-4, segments 5-10 in either the normal or inverted order, depending upon the point of rupture, and segments 4 and 3 in duplicate. The other broken chromatid will have only the proximal segments 1 and 2. Both are deficient for segment 11, which is in duplicate in the acentric fragment. If the basal megaspore receives the chromatid deficient for only segment 11, it may develop into a viable embryo sac. Microspores of similar

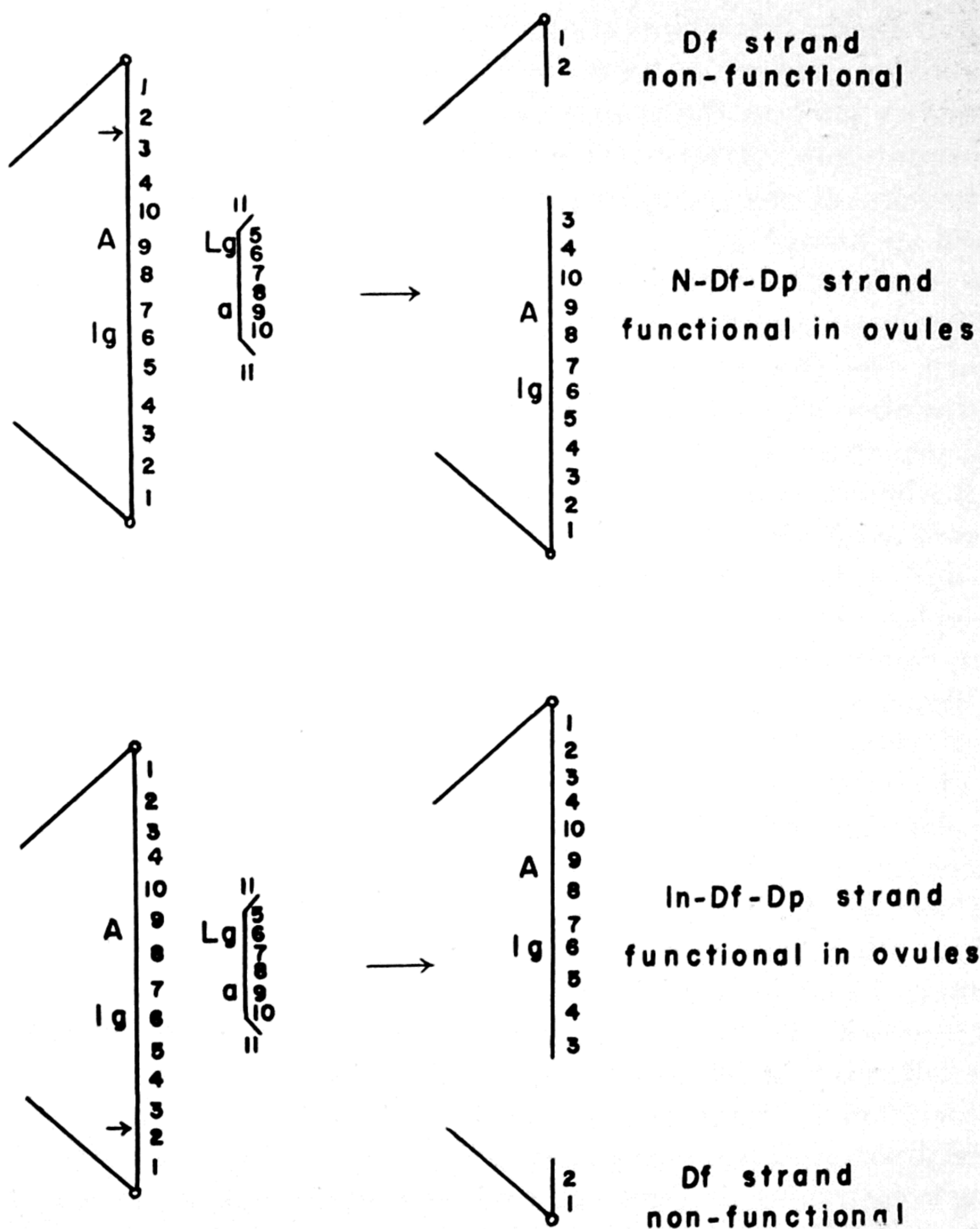


FIG. 17. *Top.* Diagram of dicentric chromatid and acentric fragment produced by a single exchange in paracentric inversion 3a. The position of bridge breakage is indicated by arrow. The constitution of the two broken chromatids is shown. The longer of the two has segments 1 to 10 in a normal order but has segments 4 and 3 in duplicate. *Bottom.* Similar to above except that position of breakage produces a broken chromatid with segments 10 to 5 in an inverted order.

constitution may develop into viable pollen grains, but such grains are not able to compete successfully in fertilization with normal grains. However, as Fig. 18 illustrates, the continuation of the bridge-breakage-fusion cycle throughout the gametophytic mitoses makes it possible for the egg nucleus to receive a chromosome with certain regions in duplicate or in even higher degrees of replication. Although the bridge-breakage-fusion cycle persists in the endosperm mitoses when the polar

nuclei bring in a chromosome with a newly broken end, there is a healing of the ends of newly broken chromosomes brought into the zygote by the egg. It behaves thereafter as a stable end and the chromosome is no longer involved in a bridge-breakage-fusion cycle. Transmissible

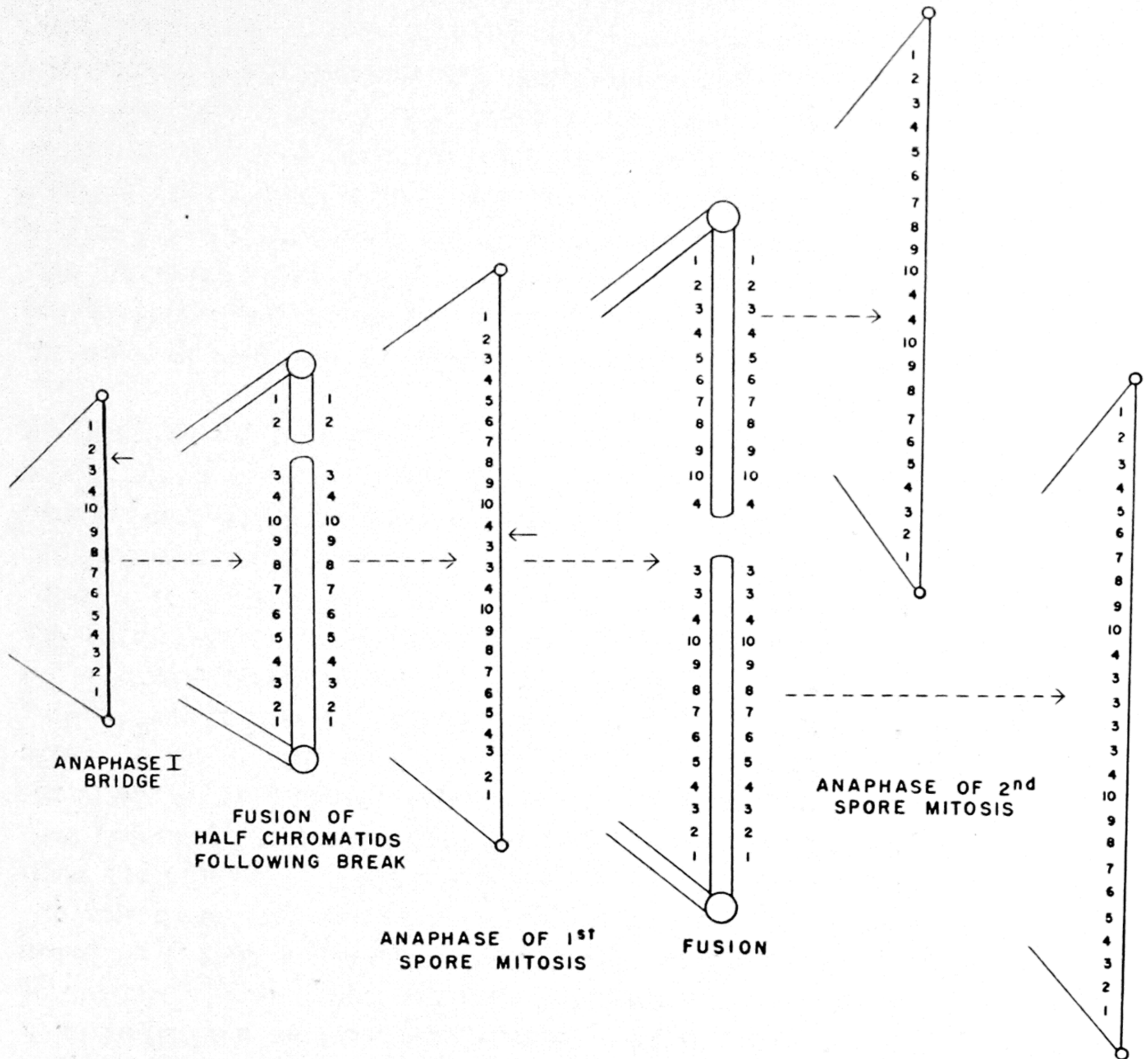


FIG. 18. Diagram of bridge-breakage-fusion cycle following formation of dicentric chromatid by crossing over in inverted segment. Position of bridge breakage indicated by solid arrows. Since the place of rupture of the bridge at anaphase I occurred near the upper centromere the bottom chromatid has segments 1 to 10 in the normal order.

deficient-duplicate chromosomes arising from inversion bridges by the above mechanism have been described by Rhoades and Dempsey (1953). Such chromosomes would not be recovered from those inversions where the missing distal segment carried genes essential for gametophytic development.

Deficient-duplicate chromosomes arising in megasporocytes with

single dicentric bridges will not be included in the basal megaspore if the bridge chromatin is selectively eliminated from the terminal nuclei by the mechanism suggested by Sturtevant and Beadle (1936) to account for the absence of egg and larval mortality following single crossovers in paracentric inversions in *Drosophila*. The low ovule abortion found by Russell and Burnham (1950) for In2c and by Morgan (1950) for In4a suggests that this mechanism operates for these paracentric inversions. However, Rhoades and Dempsey (1953) working with In3a found that the frequency of transmissible deficient-duplicate chromosomes was too high to come only from four-strand doubles within the loop or from three-strand doubles giving a single bridge at anaphase II. This, in conjunction with a higher than expected percentage of ovule abortion, forced them to conclude that many of the breakage products of single dicentric bridges at anaphase I were included in the basal megaspore.

Pericentric inversions in maize have been studied by McClintock (1931, 1933), Anderson (1936), Clark (1942), Morgan (1950), and Burnham (1950). Longley (1950) lists a number of radiation-induced inversions of both types, but most of these have not yet been thoroughly analyzed. The pachytene loops of heterozygous pericentric inversions include the centromere. When the break points in the two arms are not the same distance from the centromere, the arm ratio of the inverted chromosome is modified. Since the centromere lies within the loop of pericentric inversions, crossing over does not give rise to the dicentric bridges and acentric fragments of paracentric inversions. Genetic recombination is effectively suppressed for loci within the inverted segment because the products of single exchanges are chromatids with some loci deficient and others in duplicate. As is true for paracentric inversions, only double-crossover chromosomes are recovered; these come from two- and three-strand double exchanges. Since it is a matter of chance whether or not the basal megaspore receives a normal or a deficient chromatid following crossing over, the percentage of pollen and of ovule abortion is the same in pericentric inversions if there is no difference in the frequency of crossing over in male and female flowers. This is in contrast with the low ovule abortion of paracentric inversions where the complete or partial selective elimination of the crossover chromatids from the basal megaspore results in ovule abortion coming only or chiefly from four-strand doubles within the loop and from three-strand doubles with one exchange in the loop and one in the proximal region.

The arm ratio of chromosome 4 in most races of corn is 1:1.6, but in one strain studied by McClintock (1933) the ratio of the short to the

long arm was 1:2. The inversion loop occasionally observed at pachytene in heterozygous plants suggested that the change in arm ratio was caused by a short pericentric inversion involving unequal segments on each side of the centromere. A slight shift in the centromere location of chromosome 2 has been found in a few strains; this is undoubtedly due to a small pericentric inversion. These inversions are so short that they would not be recognized by the usual genetic tests; they were identified only by the new location of a cytological marker, the centromere or, as was true for chromosome 4, by loop formation in heterozygous plants. Although long inversions are rarely encountered, it is possible that short inversions are widespread in different populations of maize but have escaped detection.

Inversions in maize are followed in genetic studies by the aborted pollen produced by crossing over within the inversion loop. If the inverted segment is short, there will be a low percentage of aborted pollen because of infrequent crossing over. Consequently it is technically difficult to follow small inversions in linkage studies, and indeed it is difficult to detect them even by direct cytological examination. Conversely, the longer the inversion, the more frequent is crossing over and the more accurate is the classification for the presence of the inverted chromosome on the basis of pollen abortion.

In *Drosophila* there is not only a suppression of genetic recombination within the inversion, but there is also a reduction in crossover values for adjacent regions. In maize inversions, however, there is no evidence of a reduction in crossing over for adjacent regions. In fact the available data show in some instances a marked increase in these regions. Apparently a fundamental difference exists between maize and *Drosophila* in the effect of heterozygous inversions on crossing over in adjacent regions.

Although inversions can be employed in the cytological placement of genes in the physical chromosome, they have not been extensively utilized for this purpose. However, in 1938 Dobzhansky and Rhoades suggested the use of paracentric inversions as a method for locating genes affecting agronomic characters such as yield. The advantage of paracentric inversions in this connection stems from the fact that all of the loci included within the inverted sector are inherited as a block except for rare double crossovers. If strains homozygous for different inversions are crossed with elite inbred lines and the F_1 plants backcrossed to the inversion parent, two kinds of zygotes are produced: those with two inverted chromosomes and those carrying both the inverted and the normal chromosome, derived from the inbred parent. These two classes can be recognized by the absence or presence

of aborted pollen resulting from crossing over if mutant markers are not available. The two classes are classified for the agronomic character under investigation, and any significant difference between them can be properly ascribed to the genes located in the chromosome segment under experimental control. That this method can be successfully employed in a segment-by-segment analysis of the genotype of an inbred line is suggested by the results of Sprague (1941) on In5a and by unpublished data from our laboratory at Urbana using In3a. Owing to their lower ovule sterility, paracentric rather than pericentric inversions should be used in the localization of genes affecting grain yield.

IX. Deficiencies

Since cytogenetical studies on deficiencies have been presented in Section VI, 6, the discussion here will be limited to McClintock's

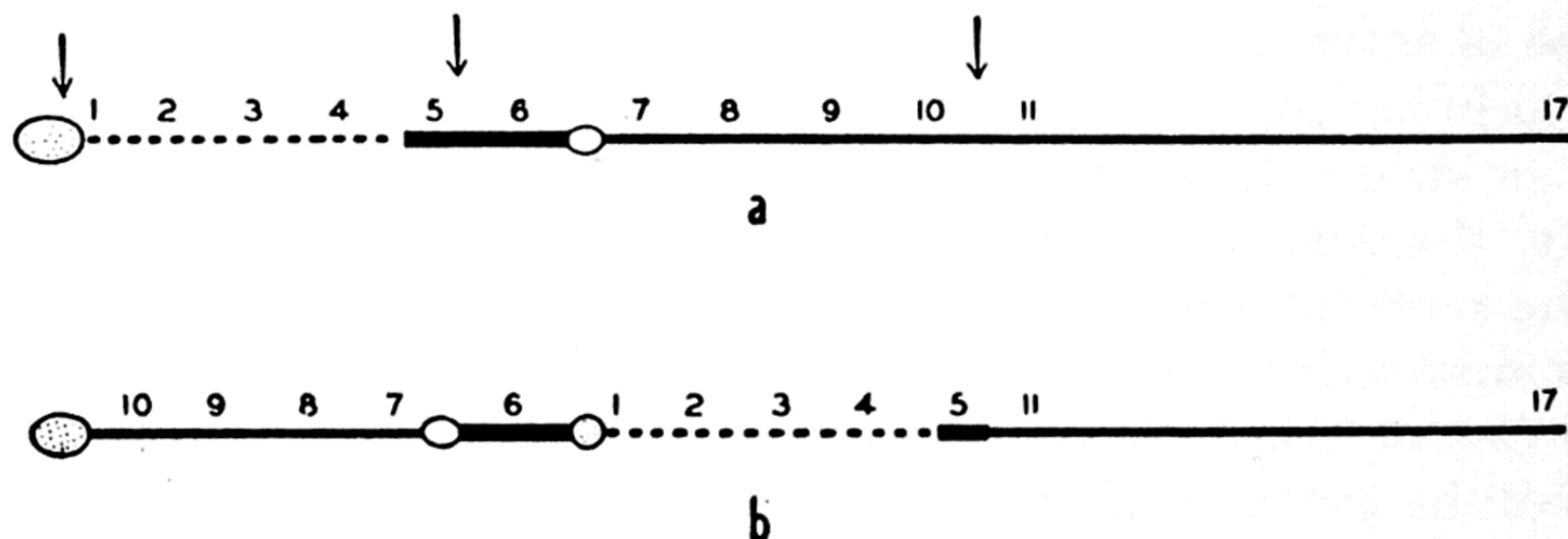


FIG. 19. *a*. A normal chromosome 9 terminating in a large knob (stippled). The clear oval region represents the centromere. The individual parts of the chromosome have been numbered from 1 to 17. The broken line (segments 1 to 4) represents the widely spaced small chromomeres of the distal two-thirds of the short arm. The wide line (segments 5 and 6) represents the proximal deep-staining region of the short arm adjacent to the centromere. The long arm is represented by a narrow line. The arrows point to the positions of breaks which resulted in the rearranged chromosome shown in *b* (from McClintock, 1941b).

(1941b, 1944) investigations on the small terminal deficiencies arising in plants heterozygous for rearranged chromosomes 9. Although her studies included a number of structurally different chromosomes 9, we shall consider only one of these in detail.

The rearranged chromosome 9 illustrated in Fig. 19*b* was derived from X-ray treatment. The large terminal knob on the short arm was broken into two parts. The proximal segment of the knob and three-fourths of the short arm were inserted into the long arm in a normal order. The section 6 to 10 was placed adjacent to the distal portion of the knob but in an inverted order. The kind of pairing found at pachynema in plants with this rearranged 9 and a normal 9 is shown

in Fig. 20. Dicentric chromatids are produced at anaphase I as the consequence of crossovers in regions *A*, *B*, and *C*. In the dicentric bridges (Fig. 21) at anaphase I produced by crossing over in region *A* the segment of chromatin lying between the two centromeres contains all of the genes of the short arm in addition to possessing in duplicate the proximal part of the knob and the proximal fourth of the short arm.

If the bridge is broken during anaphase I at position (*a*), the bottom chromatid has a full genic complement, since it lacks only the unessential knob. A break at position (*b*) produces a chromatid deficient for segment 1, whereas a break at position (*c*) yields a chromatid lacking both segments 1 and 2. Fusion occurs between the two

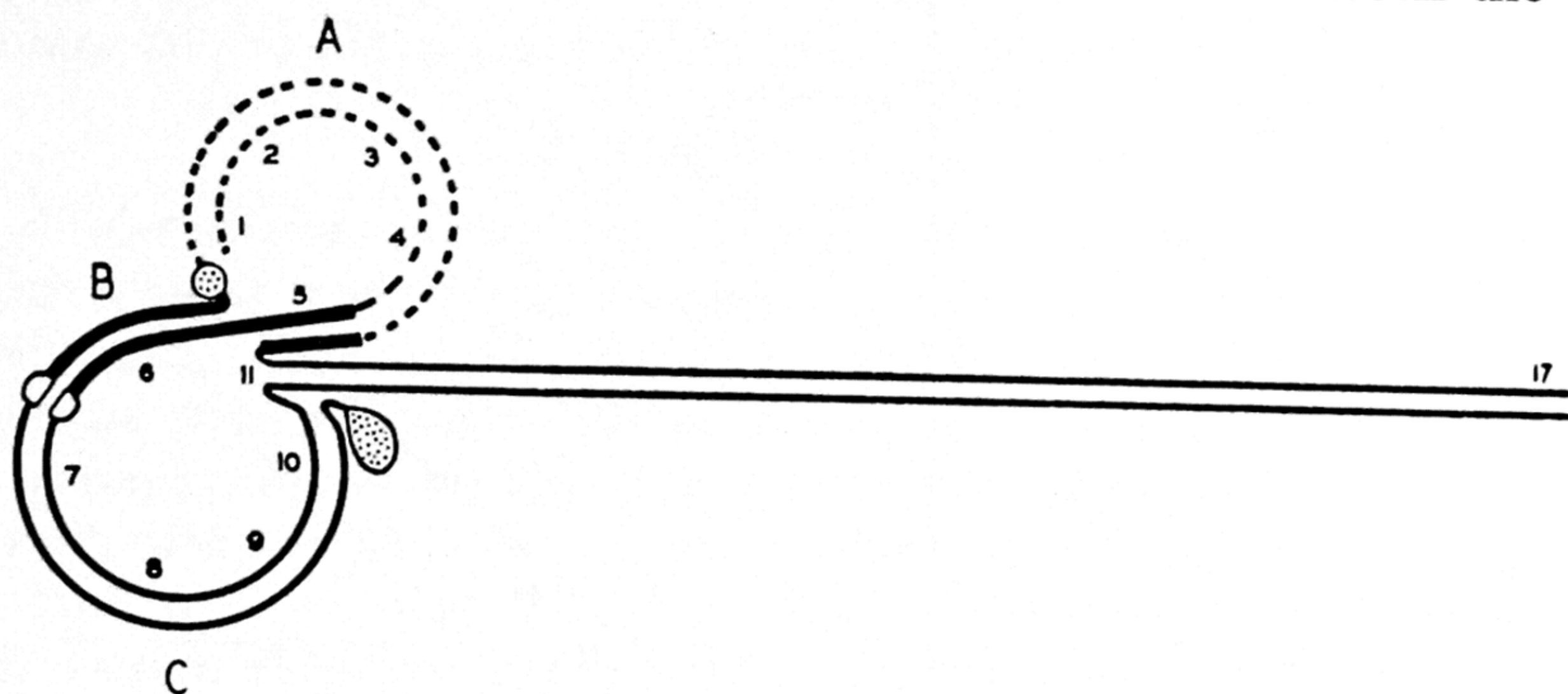


FIG. 20. Synaptic configuration produced following homologous associations of a normal chromosome 9 (without a knob) and the rearranged chromosome diagrammed in *b* of Fig. 19. Region *A* includes segments 1 to 5. Region *B* includes segment 6 (between the small knob and the centromere). Region *C* includes segments 7 to 10 (from McClintock, 1941b).

half-chromatids of each broken chromatid to produce a dicentric chromosome which will form a chromatin bridge at the first spore mitosis. This bridge will also be ruptured at anaphase followed by fusion of broken ends to form another dicentric chromosome which will again produce a bridge at the second spore division. This bridge-breakage-fusion cycle continues throughout the gametophyte mitoses so that the resulting egg and sperm nuclei possess a chromosome 9 with a freshly broken end. These may be duplicate or deficient for segments of varying extent depending upon the positions of breakage in the different mitoses, but in some cases sperm and egg nuclei will carry chromosomes 9 with broken ends which are deficient for minute terminal portions of the short arm. Although the bridge-breakage-fusion cycle continues throughout the endosperm divisions, the broken ends heal when a sperm or egg nucleus delivers a chromosome with a broken

end into the zygotic nucleus. These chromosomes no longer undergo the bridge-breakage-fusion cycle and behave as normal rod chromosomes.

McClintock (1944) obtained seven chromosomes 9 which were deficient only for the threadlike stalk connecting the terminal chromomere to the knob and six which were deficient for this stalk and for a portion of the ultimate chromomere. The deficient chromatin was not

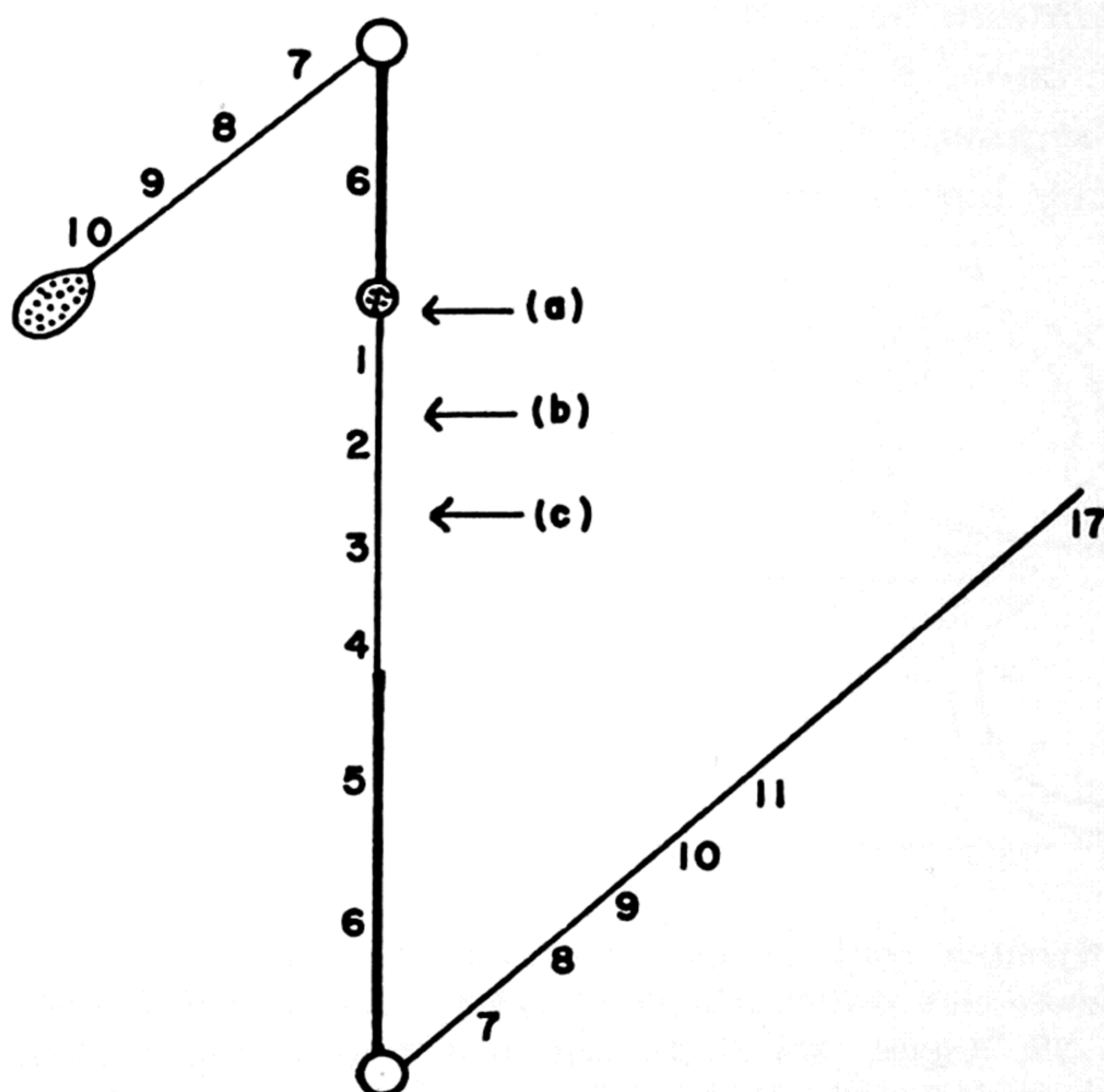


FIG. 21. Diagram of dicentric chromatid produced by crossing over in region A of Fig. 20. The segment of chromatin lying between the two centromeres contains all of the genes of the short arm in addition to possessing in duplicate the proximal part of the knob and the proximal fourth of the short arm.

essential for normal gametophyte development, since transmission of the deficient chromosomes through both male and female gametophytes proved to be normal. Plants homozygous for the chromosome 9 lacking only the terminal stalk were pale yellow (*pyd*) rather than green, whereas those homozygous for the slightly longer deficiency were devoid of both chlorophyll and carotenoids (*wd*). The recessive *yg₂* mutant, giving yellow-green plants, is situated in the ultimate chromomere. Combinations of the two kinds of deficient chromosomes 9 with each other and with normal chromosomes with the *yg₂* allele or the normal allele of this locus disclosed that all combinations with a normal *Yg₂* chromosome gave green seedlings, the *pyd/wd* combination produced a pale yellow seedling, the *yg/wd* combination a yellow-

green phenotype, but that the *yg/pyd* combination gave green seedlings.

The pale yellow color of the *pyd/wd* combination and the yellow-green color of the *yg/wd* combination indicated allelism of *pyd* and *yg* with *wd*, but since normal green seedlings were found for the *yg/pyd* combination, *pyd* and *yg* are not allelic to each other. If it were not known from the cytological observations that the *pyd* and *wd* phenotypes were due to homozygous deficiencies and not to mutant genes, it could be argued that in this constellation of genetic effects there were two series of alleles, one consisting of *green*, *yg* and *wd*, and the other of *green*, *pyd* and *wd*. The nonlinear effect produced by the *yg/pyd* combination would be ascribed to pseudo-allelism.

X. Ring Chromosomes

Brief mention has already been made of the structural alterations which ring chromosomes occasionally undergo in somatic mitoses. McClintock (1932, 1938b, 1941a) studied two rings involving segments from the proximal region of the short arm of chromosome 5. Both of these were induced by breaking a normal chromosome 5 with X-rays. In each case one break occurred in the centromere, which was fractured into two portions, and the second point of breakage was in the short arm. Fusion of broken ends resulted in the formation of a ring chromosome with one part of the broken centromere and of a deficient rod possessing the remaining portion of the fractured centromere. The centromeres of both rod and ring chromosomes were able to function normally. Plants were obtained with two deficient rods and one (or more) ring chromosomes. Since the chromatin of the ring chromosome was composed of that missing from the deficient rod chromosome, the young sporophytes initially were normal in appearance but soon manifested sectors of various kinds of mutant tissue. Cytological observations revealed that the ring chromosome was not present unaltered in all cells but that some cells had larger rings with certain segments in duplicate. Others had smaller rings deficient for certain portions originally present in the ring, and in some cells the ring chromosome had been completely eliminated.

These modified ring chromosomes arise in the following way. In some mitotic prophase, as the probable consequence of somatic sister-strand crossing over, the two halves of a divided ring chromosome form either a continuous dicentric double-sized ring or two interlocked rings instead of two separate monocentric ring chromosomes. The movement of the two centric regions to opposite poles at anaphase produces a chromatin bridge which remains suspended on the central por-

end into the zygotic nucleus. These chromosomes no longer undergo the bridge-breakage-fusion cycle and behave as normal rod chromosomes.

McClintock (1944) obtained seven chromosomes 9 which were deficient only for the threadlike stalk connecting the terminal chromomere to the knob and six which were deficient for this stalk and for a portion of the ultimate chromomere. The deficient chromatin was not

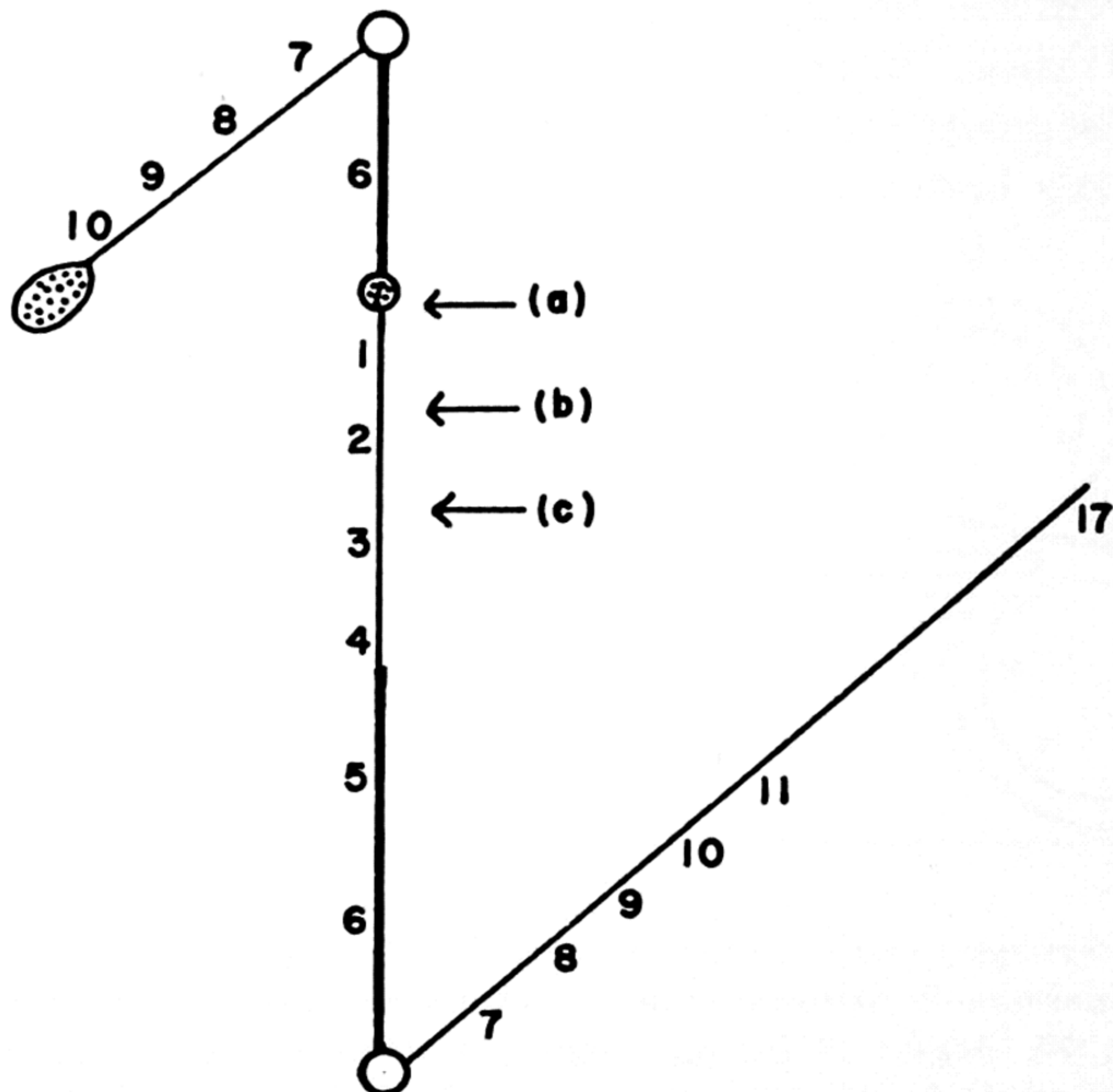


FIG. 21. Diagram of dicentric chromatid produced by crossing over in region A of Fig. 20. The segment of chromatin lying between the two centromeres contains all of the genes of the short arm in addition to possessing in duplicate the proximal part of the knob and the proximal fourth of the short arm.

essential for normal gametophyte development, since transmission of the deficient chromosomes through both male and female gametophytes proved to be normal. Plants homozygous for the chromosome 9 lacking only the terminal stalk were pale yellow (*pyd*) rather than green, whereas those homozygous for the slightly longer deficiency were devoid of both chlorophyll and carotenoids (*wd*). The recessive *yg₂* mutant, giving yellow-green plants, is situated in the ultimate chromomere. Combinations of the two kinds of deficient chromosomes 9 with each other and with normal chromosomes with the *yg₂* allele or the normal allele of this locus disclosed that all combinations with a normal *Yg₂* chromosome gave green seedlings, the *pyd/wd* combination produced a pale yellow seedling, the *yg/wd* combination a yellow-

green phenotype, but that the *yg/pyd* combination gave green seedlings.

The pale yellow color of the *pyd/wd* combination and the yellow-green color of the *yg/wd* combination indicated allelism of *pyd* and *yg* with *wd*, but since normal green seedlings were found for the *yg/pyd* combination, *pyd* and *yg* are not allelic to each other. If it were not known from the cytological observations that the *pyd* and *wd* phenotypes were due to homozygous deficiencies and not to mutant genes, it could be argued that in this constellation of genetic effects there were two series of alleles, one consisting of *green*, *yg* and *wd*, and the other of *green*, *pyd* and *wd*. The nonlinear effect produced by the *yg/pyd* combination would be ascribed to pseudo-allelism.

X. Ring Chromosomes

Brief mention has already been made of the structural alterations which ring chromosomes occasionally undergo in somatic mitoses. McClintock (1932, 1938b, 1941a) studied two rings involving segments from the proximal region of the short arm of chromosome 5. Both of these were induced by breaking a normal chromosome 5 with X-rays. In each case one break occurred in the centromere, which was fractured into two portions, and the second point of breakage was in the short arm. Fusion of broken ends resulted in the formation of a ring chromosome with one part of the broken centromere and of a deficient rod possessing the remaining portion of the fractured centromere. The centromeres of both rod and ring chromosomes were able to function normally. Plants were obtained with two deficient rods and one (or more) ring chromosomes. Since the chromatin of the ring chromosome was composed of that missing from the deficient rod chromosome, the young sporophytes initially were normal in appearance but soon manifested sectors of various kinds of mutant tissue. Cytological observations revealed that the ring chromosome was not present unaltered in all cells but that some cells had larger rings with certain segments in duplicate. Others had smaller rings deficient for certain portions originally present in the ring, and in some cells the ring chromosome had been completely eliminated.

These modified ring chromosomes arise in the following way. In some mitotic prophase, as the probable consequence of somatic sister-strand crossing over, the two halves of a divided ring chromosome form either a continuous dicentric double-sized ring or two interlocked rings instead of two separate monocentric ring chromosomes. The movement of the two centric regions to opposite poles at anaphase produces a chromatin bridge which remains suspended on the central por-

tion of the spindle after the rod chromosomes have completed their poleward journey. As is illustrated in Fig. 22, breakage may occur in the dicentric bridge from tension produced by centric pull. A portion of the broken double-sized ring goes to each pole. Fusion occurs between

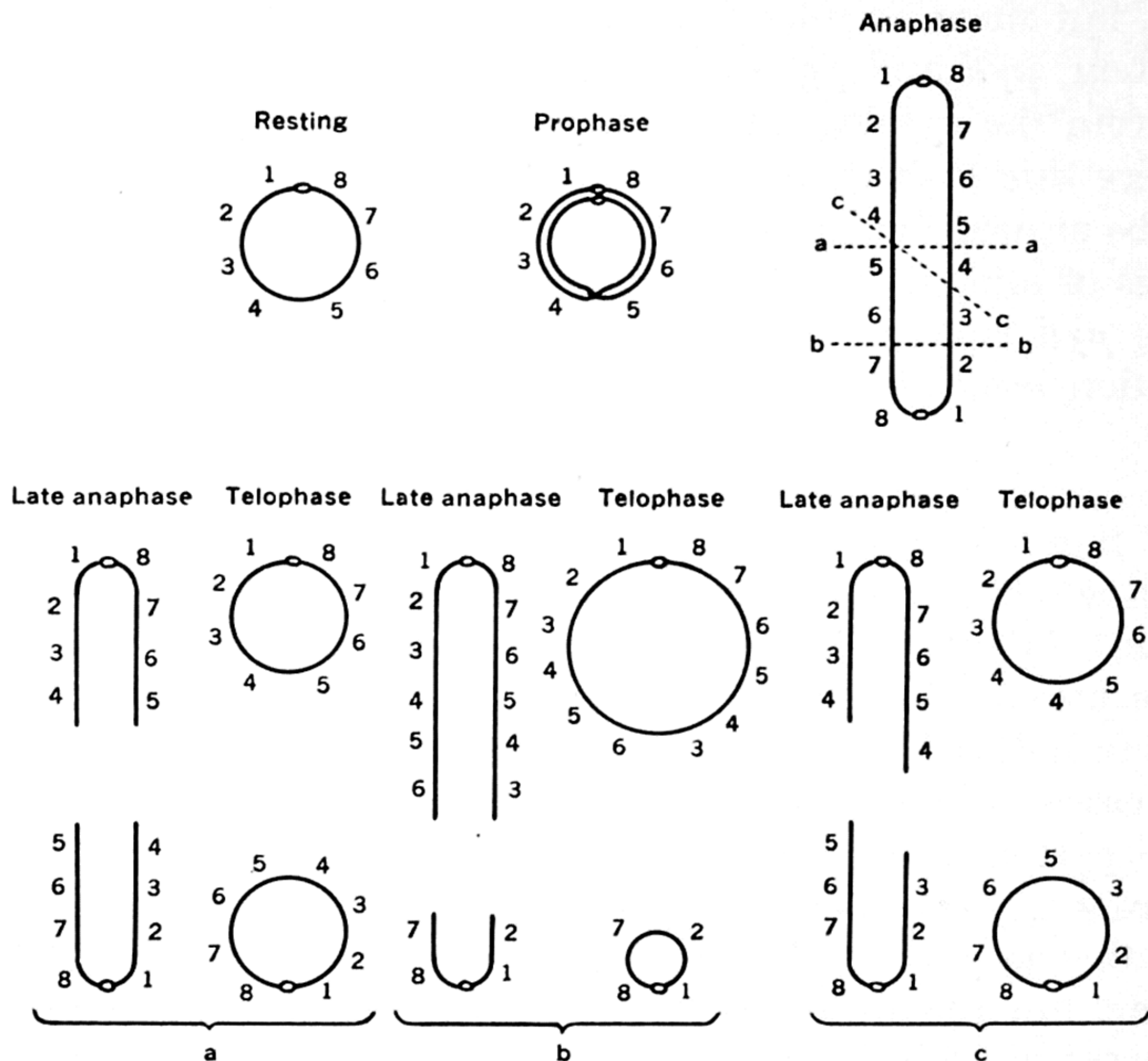


FIG. 22. Diagram illustrating a method by which a ring chromosome becomes altered in chromatin constitution. *Upper left:* A ring chromosome in a resting nucleus. The clear oval represents the centromere. The individual parts of the ring chromosome are designated by the numerals. *Upper middle:* A prophase configuration following a "crossover" between two sister chromatids of the divided ring chromosome. A dicentric, double-sized ring chromosome is produced. *Upper right:* Appearance of the dicentric ring chromosome in the following anaphase. Breakage of the chromatin strands between the centromeres may occur at any position. Three possible positions, *a*, *b*, and *c*, respectively, are indicated by the dash lines. The resulting broken strands at late anaphase and the new ring chromosomes formed at telophase by fusions of broken ends of these strands are diagrammed below in the bracketed figures for the breaks, *a*, *b*, and *c*, respectively (from McClintock, 1941a).

the two broken ends, giving rise to another ring chromosome. The constitution of these newly formed rings depends upon the position where the double-sized ring was broken. Unequal breakage leads to one ring with duplicated segments and one deficient for the segments in duplicate in the other ring. The extent of the duplications and deficiencies varies greatly. McClintock (1938b, 1941a) found that plants with mutant sectors carried deficient ring chromosomes. The kind of

mutant characteristic depended upon the particular chromatin segment which had been deleted from the ring. Inasmuch as the two rod chromosomes lacked the chromatin of the original ring chromosome, tissues with deficient rings were homozygous deficient for certain loci. The loss of one locus from the ring produced a specific effect, and the loss of a different locus gave rise to a different phenotype. If the two loci were missing from the same ring, then the deficient tissue manifested both mutant phenotypes. In this study it was first demonstrated that the effect of a homozygous deficiency resembled that produced by a known recessive gene. Different parts of the same plant could have smaller rings of unlike constitution, and it would be a mosaic of different mutant phenotypes.

More recently Schwartz (1953a) studied a large ring chromosome involving most of chromosome 6 (see Section VI, 5). This ring was also somatically unstable and gave rise to larger and smaller rings by the same mechanism elucidated by McClintock's earlier work. Segments of the ring were transferred to a normal rod chromosome by two- and three-strand double exchanges of meiosis in ring/rod heterozygotes. Rod chromosomes with duplicated segments arose from breakage of the single dicentric bridges at anaphase I followed by healing of the broken ends in the zygote—a mechanism which had been shown by McClintock (1941b) to occur. From plants heterozygous for a normal rod and one with duplicated segments ring chromosomes were again produced as the result of pairing and crossing over involving the duplicated segment. This reconversion of a rod back to a ring completed a ring-rod-ring cycle.

XI. Abnormal Chromosome 10

An abnormal type of chromosome 10 is found in some strains of maize from Latin America and the southwestern United States (Longley, 1937, 1938) which differs from the usual or normal chromosome 10. The short arms show no morphological differences, and the chromomere pattern in the long arms of normal and abnormal 10 is identical throughout the proximal five-sixths, but in the distal one-sixth of abnormal 10 there are three large and distinct chromomeres (or small knobs?) not found in the corresponding section of normal 10. The most distal of these large chromomeres lies very near the end of the long arm of normal 10. More obvious than the difference in chromomere pattern, however, is the extra segment of chromatin present in abnormal 10. Beginning at the point lying just beyond the last prominent chromomere there is a light-staining euchromatic region comprising somewhat less than half of the length of the extra segment, next a

large block of heteropycnotic chromatin, and then a small terminal euchromatic segment with small and diffuse chromomeres (Fig. 23A). In plants heterozygous for the two kinds of chromosome 10 there is no evidence of a reduction in crossing over in the proximal portion of the long arm, but crossing over is infrequent or nonexistent in the distal one-sixth with a dissimilar chromomeric structure.

It was shown by Rhoades (1942) that abnormal 10 was preferentially segregated to the functional basal megaspore during megasporogenesis in plants heterozygous for the two kinds of chromosome 10. Approximately 70 per cent of the basal megaspores possessed an abnormal 10 instead of the 50 per cent expected with random segregation. The genetic factor or factors responsible for preferential segregation are located either in the distal region of unlike chromomeres or in the large terminally attached piece of extra chromatin; it will not be possible to tell where they lie until the two regions become separated by crossing over or by chromosome breakage. Since it is the terminal portion of abnormal 10 which determines preferential segregation, it follows that loci near the end of the long arm of chromosome 10 will undergo preferential segregation more frequently than will more proximally located loci because the more crossing over there is, the weaker will be the association of a given locus with the terminal chromatin segment. The *R* locus, which was known from other studies to occupy a distal position in the long arm, was very closely linked to the terminal segment and had a higher degree of preferential segregation than did the more proximally located *g₁* and *li* loci.

Preferential segregation in heterozygous plants occurs as the consequence of a crossover between the centromere and the terminal segment. When there is one exchange in the long arm, each of the two disjoining dyads at anaphase I possesses one normal chromatid 10 and one abnormal chromatid 10. Preferential segregation is restricted to the second meiotic division and is the result of the heteromorphic dyads becoming oriented on the spindle at metaphase II in such a way that the abnormal chromatids pass to the two terminal poles of the linear set of four megaspores while the two normal chromatids go to the two inner poles. Normal segregation occurs when the dyads are homomorphic.

Longley (1945) made the important discovery that in plants heterozygous for abnormal 10, chromosome pairs other than chromosome 10 were also preferentially segregated when one of the two homologues had a knob and the other was knobless. Normal segregation was found for the heteromorphic bivalents if normal 10 was homozygous. Data were obtained for both chromosomes 9 and 6, but his data on 9

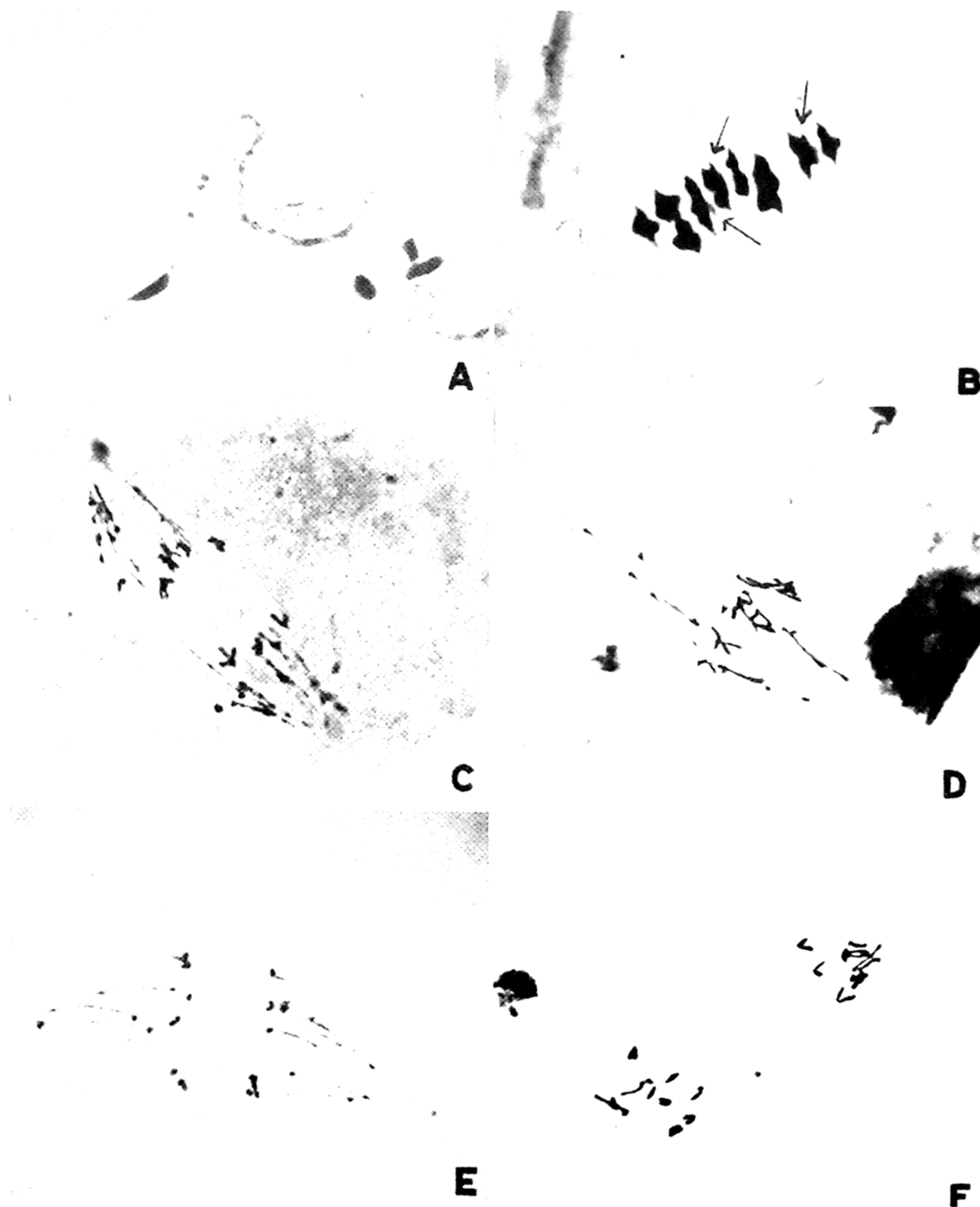


FIG. 23. Photomicrographs at meiosis in plants homozygous for abnormal chromosome 10. All are from propionic carmine smear preparations.

A. Pachynema. Note the large heterochromatic knob in the extra segment.

B. Metaphase I. The 10 bivalents are normally co-oriented on the spindle. Neo-centromeres are arising from the regions indicated by arrows. The third and fourth bivalents from the right are somewhat superimposed.

C. Anaphase I. Some of the disjoining dyads are normal, but in most the neo-centric regions are pulling the ends of the arms to the poles in advance of the rest of the chromosome.

D. Metaphase II. Precocious poleward movement of neo-centric regions has occurred before true centric region has divided.

E. Early anaphase II. The monads with precocious neo-centric regions are moving poleward in advance of the other dyads.

F. Late anaphase II. Note the inverted V-shaped monads.

are more extensive. Some chromosomes 9 have a terminal knob on the short arm, whereas others are knobless. The *C*, *Sh*, and *Wx* loci lie in the short arm, with *Wx* nearest the centromere and *C* in the most distal position. There is about 44 per cent recombination between *Wx* and the knob, while *C* and *Sh* are 23 and 26 recombination units, respectively, from the knob. Plants heterozygous for abnormal 10 and of knob-*C*/knobless-*c* constitution were used as the female parent in crosses with recessive *c* pollen. Instead of the expected 1:1 ratio for *C*:*c*, Longley (1945) found that 64 per cent of the functioning megaspores carried the *C* allele. The *Sh* locus, which is closely linked with *C*, showed a similar amount of preferential segregation in comparable tests, but the *Wx* locus, which is distantly removed from the knob, gave little evidence of being preferentially segregated. This progressive decrease in the extent of preferential segregation is expected if the terminal knob is instrumental in producing nonrandom segregation, since the closer a locus is to the knob, the greater would be the distortion from a normal 1:1 ratio. Previous to this finding the heteropycnotic knobs had been considered as genetically inert, but it now appears that this is not wholly true.

Rhoades and Vilkomerson (1942) reported that abnormal 10 not only produced preferential segregation but was responsible for the formation of neo-centromeres at both meiotic divisions. Chromosomal or half-spindle fibers arose at metaphase from regions other than the true centric region in many of the tetrads of the first division and the dyads of the second division in plants homozygous or heterozygous for abnormal 10 (Figs. 23*B* and *D*). The neo-centromeres moved poleward more rapidly than the true centric regions, thus producing anaphase I dyads and anaphase II monads whose free ends reached the poles in advance of the rest of the chromosome (Figs. 23*C*, *D*, and *F*).

The number of chromosomes with neo-centromeres is correlated with the number which possess knobs and it is likely that the precociously acting neo-centromeres arise near the distal ends of knob-bearing arms. It has been suggested (Rhoades, 1952) that the formation of neo-centromeres is responsible for preferential segregation. The hypothesis, which applies to chromosome 10 as well as to all bivalents heterozygous for knobs, is as follows. It should be recalled that the two spindles of the second meiotic division of megasporogenesis are arranged in a linear order. Assume a bivalent composed of one knobbed and one knobless chromosome. Abnormal 10 is also present. If a crossover occurs between the knob and the centromere, the anaphase I dyads each consist of one knobbed and one knobless chromatid. In each dyad it is the knob-bearing arms which form the neo-centric regions and which pull the dyads

poleward; the knobbed chromatid consequently would lie closer to the pole while the knobless chromatid would face the spindle plate. If the orientation of the two chromatids was maintained through interphase, it would result in the dyads of each daughter cell becoming oriented on the metaphase II spindle in such a way that the two knobbed chromatids would disjoin to the terminal poles while the two knobless chromatids would pass to the two inner nuclei of the linear set of four. The excess of basal megaspores with a knobbed chromatid over those with a knobless chromatid would be determined by the frequency of heteromorphic dyads resulting from crossing over between the knob and centromere. This putative mechanism satisfactorily accounts for all cytological and genetic facts.

XII. Mutation

Since this chapter is concerned with the cytogenetics of maize, we shall exclude from the discussion of mutation many investigations which were purely genetic in nature. It is fully realized that important and valuable studies will receive no or little mention, but a complete account of mutational investigations could hardly be encompassed in this survey with its emphasis on cytogenetics. Further, we shall limit ourselves to a restricted use of the term "mutation" in that only gene and point mutations will be considered.

As Sturtevant has said "Mutations are accidents and accidents happen." It lies within the province of cytogenetics to determine the nature of the genetic changes which constitute or which simulate gene mutation. In many instances these "mutations" have been shown to be due to extragenic changes. They may be produced by deficiencies (for example, the *pyd* and *wd* mutants whose breeding behavior is precisely that of true gene mutations), by duplications (where genic unbalance or possibly position effect produces a mutant phenotype whose inheritance follows Mendelian laws when the duplicated segment is incorporated into an otherwise normal chromosome), by small rearrangements leading to position effects, by position effects which involve nothing more than a recombination of genic elements by crossing over, and even by the separation through crossing over of the component parts of a compound locus.

When any given mutation cannot be shown to be due to any of the above extragenic causes, and it should be recognized that the cytological detection of small deficiencies or minute rearrangements is often difficult or impossible, then this mutation is relegated to the class of gene mutation. Since this classification rests upon our ability to discriminate between the various mechanisms and since our discriminatory powers

are limited at best, there is always the suspicion that more refined investigations of an apparent gene mutation will disclose its extragenic origin. It is doubtful if any mutation can with certainty be said to represent a gene mutation in the classical sense of the term. The facts of organic evolution would seem to demand that intragenic mutations occur. Such mutations, however, cannot be distinguished with the methods now available from other highly localized heritable variations.

The complexity of the mutation problem may be illustrated by the following example. In the Black Mexican strain of sweet corn the dominant A_1 allele mutated to recessive a_1 . The recessive a_1 allele was extremely stable, there being no evidence that it, or other a_1 alleles, ever underwent reverse mutation in either somatic or germinal tissue. It was found, however, that the Dt locus situated in or adjacent to the heterochromatic knob on the short arm of chromosome 9 induced the normally stable a_1 alleles to mutate with an extremely high frequency to higher alleles, many of them being to the highest level in the series (Rhoades, 1938, 1941b). Since the recessive a_1 allele was derived by mutation from A_1 and since it was able in the presence of Dt to mutate back to A_1 , it could be argued that here, at least, we were dealing with true gene mutation. There was no evidence that the Dt gene was changed in any way in those nuclei where a_1 was induced to mutate back to A_1 ; thus there was no transference of gene substance from the Dt to the a_1 gene. The ability of a_1 to mutate to A_1 clearly indicated that the original change of A_1 to a_1 was not associated with deficiency. Until recently there was no evidence of position effect in maize; thus it appeared highly unlikely that mutant effects associated with duplications or rearrangements were involved. Since mutation of a_1 to A_1 occurred in somatic cells, there was no reason to assume that a recombination of genic elements or a separation of the components of a compound locus was concerned, since these occur by meiotic crossing over. Inasmuch as all known extragenic mechanisms for genetic changes simulating gene mutation apparently were not responsible, it could be concluded that in the a_1 - Dt case we were dealing with true gene mutation. This may yet be the case, but recent studies by McClintock on mutable genes offer another explanation.

McClintock (1950, 1951) found a number of newly arisen mutable loci in the progenies of self-pollinated plants in which the short arms of chromosomes 9 had undergone the chromosomal type of bridge-breakage-fusion in early sporophytic mitoses. (The chromosome type of bridge-breakage-fusion is produced when both the egg and sperm nuclei contribute a chromosome with a freshly broken end, derived from the chromatid type of bridge-breakage-fusion in the preceding

gametophytic mitoses, to the zygotic nucleus. Fusion occurs between the two sister chromatids of each broken chromosome, and each forms a dicentric bridge at the first zygotic anaphase. Following breakage of the two chromatin bridges, each of the two telophasic nuclei has two chromosomes with broken ends. Fusion of broken ends of the two chromosomes, rather than healing, may occur, giving rise to a single dicentric chromosome composed of the two chromosomes derived from the egg and sperm nuclei. The succeeding sporophytic mitoses now have the chromosome type of bridge-breakage-fusion cycle, but in later divisions healing of broken ends often occurs. Two rod chromosomes, whose constitutions depend upon the preceding points of breakage, are formed, and their behavior henceforth is normal.) Subjection of the chromatin to the stress and tension of this bridge-breakage-fusion had in some way produced an unusual genetic situation, presumably an alteration in an element of the heterochromatin, which resulted in stable loci becoming highly mutable. Her mutable loci fell into two groups: (1) those whose instability depended upon another locus and (2) those whose mutability was autonomous. Her investigations have been chiefly concerned with the first group.

The first indication of some unusual genetic situation was the discovery that a high frequency of breaks was occurring in the short arm of chromosome 9 to the right of the *wx* locus. Endosperms of *C wx/C wx/I Wx* constitution, which should have colorless aleurone because of the dominant *I* allele at the *C* locus and blue-staining starch because of the presence of *Wx*, had many sectors with colored aleurone and red-staining starch. The loss of the *I* and *Wx* alleles came from breakage to the right of *Wx* followed by the elimination of the acentric fragment bearing these two genes. Cytological observations showed that breakage of the *I Wx* chromosome was followed by fusion of broken ends to produce an acentric and a dicentric fragment. The position where the short arm was broken was designated *Ds* for dissociation, but these breaks did not occur unless a second unit called Activator (*Ac*) was also present. The location of *Ds* proved to be inconstant in that it occasionally was shifted to other positions in chromosome 9 and even to other chromosomes. One such transposition of *Ds* placed it between the *I* and *Wx* alleles. More convincing evidence for the formation of acentric and dicentric fragments following breaks at *Ds* was obtained in kernels whose endosperms were of *C wx/C wx/I Ds Wx* constitution and which possessed the Activator locus. Breaks at *Ds* followed by fusion to give acentric and dicentric chromosomes produced an acentric piece with the *I* allele while the dicentric chromosome had two *Wx* alleles. A sector of the endosperm arising from a cell in which this occurred

would have uniformly colored aleurone, but it would be a mosaic of blue- and red-staining areas. Cells with red-staining starch came from the loss of the *Wx* allele as a consequence of unequal breaks in the chromatin bridges produced by the bridge-breakage-fusion cycle of the dicentric chromosome. McClintock (1951 and unpublished) observed all the recognizable transpositions of *Ds* in relation to the *I-Sh-Bz-Wx* genes in the short arm of chromosome 9. The recessive alleles of the gene or genes lost in the acentric fragments would give rise to the primary sectors of the kernel, whereas those genes situated on the dicentric chromosomes and undergoing a later loss through bridge-breakage-fusion cycles give rise to variegation within the original sectors. The kind of mosaic pattern is thus diagnostic of the position of the *Ds* locus.

Another kind of event besides the formation of acentric and dicentric fragments may occur following breaks at the *Ds* locus. This is designated as event 2 and consists in the elimination of the *Ds* locus from the chromosome, which remains structurally unaltered. The relative frequencies of events 1 and 2 were found to depend upon the "state" of *Ds*. Although a number of different "states" exist, it will suffice here to describe two of them. When a state-1 *Ds* is present, breakage at *Ds* results in many events 1 and in few events 2, whereas with a state-2 *Ds* the reverse is true; that is, the state of *Ds* determines which kind of event will predominate at this locus. A state-1 *Ds* occasionally changed to a state-2, but the latter never gave rise to the former. This was taken to indicate that the amount of material composing the *Ds* locus is greater in a state-1 *Ds* than in a state-2; a partial loss of *Ds* substance from a state-1 would give rise to a state-2 *Ds*. Both *Ds* and *Ac* are believed to be composed of heterochromatin. The *Ac* locus, which controls the time and frequency of changes at the *Ds* locus, also exhibits various "states"; these are recognized by differences in the time and frequency with which breaks occur at *Ds* and possibly represent quantitative differences in *Ac*.

There is a remarkable effect of varying the dosage of *Ac*. When present in a single dose the "mutations" at *Ds* are relatively few but early in endosperm development; with two doses of *Ac* the changes at *Ds* are late but numerous; whereas in endosperms with three *Ac* loci the time of mutation is so greatly delayed that it may never be realized.

Further study with the *Ds-Ac* complex revealed that transpositions of *Ds* were responsible for the origin of a host of mutable loci. This is clearly shown by McClintock's analysis of c^{m-1} . In a chromosome 9 carrying the *C* allele and with *Ds* lying slightly to the right of the *wx* locus, the *Ds* locus was removed from its original position and was in-

serted next to the *C* allele. Breaks now occurred at *Ds* in its new location while no *Ds* activity was manifest at its former position. Concomitant with the transposition of *Ds* was a change in the functioning of the *C* allele, which now behaved as a recessive *c* allele. The change was designated as c^{m-1} . In kernels homozygous for c^{m-1} and lacking *Ac* the aleurone was completely colorless; c^{m-1} behaved as a stable recessive mutant apparently no different from known recessive *c* alleles. However in the presence of *Ac*, kernels with the c^{m-1} allele had colored areas on a colorless background as if c^{m-1} were a mutable gene. The c^{m-1} gene could be described as a *c* allele which was stable with *ac*, as was a_1 with *dt*, but which became mutable with *Ac*, as did a_1 with *Dt*. McClintock (1951) found that the c^{m-1} gene was actually an inhibited *C* allele whose activity was suppressed by the adjacent *Ds* locus. Mutation of c^{m-1} involved nothing more than the loss of *Ds* from the *C Ds* complex. When *Ds* was removed from the c^{m-1} chromosome by event 2 type of *Ds* behavior, there was no longer any inhibition of the *C* allele and aleurone color was produced.

It was possible to show for other loci which suddenly became mutable in strains with *Ds* and which were *Ac* controlled that a transposition of *Ds* was associated with the origin of the mutable gene.

In the c^{m-1} situation as well as in other mutable loci which were analyzed it is clear that mutation is due to the loss of the *Ds* locus by a breakage mechanism from an inhibited dominant allele. The changes of c^{m-1} to *C* are not mutations of the gene; yet the behavior of c^{m-1} simulates that of recessive a_1 with *Dt*. It is not improbable that the recessive a_1 allele is simply an inhibited *A₁* allele and that mutation of a_1 to *A₁* involves no more than the loss of inhibiting chromatin. Since *Ds* and *Ac* presumably arose during a chromosome bridge-breakage-fusion cycle, it appeared possible that a new *Dt* locus could be created in a similar manner. From plants homozygous for a_1 and *dt* whose short arms of chromosome 9 were undergoing the bridge-breakage-fusion cycle, a number of kernels were obtained with colored areas indicative of mutation of a_1 to *A₁*. Since these colored areas occurred in the endosperm cells, no genetic tests for the presence of a new *Dt* locus could be made; the evidence for the creation of a new *Dt* is inferential but suggestive.

If mutation of c^{m-1} to *C* involves nothing more than the loss of inhibiting heterochromatin, is it possible that in other mutable loci a similar mechanism is operating? Are all mutations associated with breakage of one kind or another? There is no evidence of breakage or of transpositions in the a_1 -*Dt* case, but Brink and Nilan (1952) believe that a mutable condition at the *P* locus involves such a mechanism. Emerson (1914, 1917, 1929) found that pericarp color variegation was

due to the unstable P^{VV} allele which mutated to a P^{RR} allele giving full red pericarp color.

The data of Brink and Nilan (1952) suggest that the P^{VV} locus consists of a discrete genetic element Modulator (Mp), lying adjacent to the P^{RR} allele, which inhibits the action of P^{RR} . Removal of Modulator from the P locus restores the activity of P^{RR} so that a red sector appears. The occasional occurrence on medium-variegated ears of a new phenotype, light variegated, as a well-defined twin to the red mutation, lends support to this interpretation. It is found that the light-variegated component of the twin spots possesses an unchanged P^{VV} locus plus Modulator in a new position in the genome. This so-called transposed Modulator ($tr-Mp$) presumably is the Modulator lost from the P locus in the red co-twin at the differential somatic mitosis in which P^{VV} , in the one daughter chromatid, is changed to P^{RR} . Brink (1954a) has assayed the components of one such red-light-variegated twin spot for Mp . The latter was found to be absent from the red kernels and present in the light-variegated sector, as expected on the hypothesis. It has been shown also that transposed Modulator may be reduplicated in the genome and that the two units may occupy different positions in the complement (Brink, 1954b). A P^{VV} allele in the absence of Modulator elsewhere in the genome gives rise to a phenotype designated medium variegated, which shows a very large number of mutations to red. The same P^{VV} allele plus a single transposed Modulator results in a light-variegated phenotype, in which the frequency of mutations of P^{VV} to P^{RR} is reduced about 60 per cent. The addition of two transposed Modulators gives rise to a third variegated class called "very light" (Fig. 24). The number of P^{VV} to P^{RR} mutations in very lights, as compared with lights, is decreased approximately 87 per cent. Thus the effect of transposed Modulator in increasing dosages is to reduce the frequency of mutations of variegateds to red exponentially. Barclay (1954) has found, in the recent studies on variegated pericarp, that Modulator activates Dissociation (Ds). Thus the unit corresponds in this respect to McClintock's Activator (Ac). Mosaic pericarp, which involves another mutable P allele, does not have this action.

Studies on the mutational behavior of mosaic pericarp by Suto (1952) should be mentioned, although his analysis is not complete and his conclusions tentative. He mistakenly reported that he worked with the "Calico" type of variegated pericarp, which was the subject of Emerson's and Brink and Nilan's investigations, but in reality he was dealing with another kind of variegation known as mosaic pericarp whose breeding behavior is different from that of variegated pericarp.

His conclusions are as follows. An Enhancer (E) locus 1.5 units to the right of P has a specific modifying effect on P alleles. When E is in close proximity to any of the P alleles, even the lowest in terms of dominance, these alleles are dominant over normally higher ones. E is believed to represent a duplication of the P locus. The infrequent germinal mutations of the mosaic P allele arise, so it is argued, from



FIG. 24. Ears showing dosage effect of transposed Modulator. The leftmost ear shows the medium-grade variegation found in ears where Mp is adjacent to P^{RR} . The sector with uniformly red-colored kernels came from an early removal of Mp from the P^{RR} allele. The second ear from the left shows the light-variegated phenotype produced when Mp is adjacent to P^{RR} , and a second Mp , transposed from its original position next to P^{RR} , is present in the nucleus. The second ear from the right with the very light-variegated phenotype has three Modulators. One is adjacent to P^{RR} , but the other two have been transposed away from P^{RR} . The rightmost ear is one with colorless pericarp (courtesy of R. A. Brink).

unequal crossing over at meiosis, and the more frequent sectors producing the mosaic phenotype of the ear are believed due to unequal crossing over between sister chromatids in somatic cells. It is likely that an explanation similar to that advanced by Brink and Nilan (1952) for the variegated P allele will prove to be more nearly correct.

Peterson (1953) offers an interpretation of a mutable pale green condition which is very similar to that operating in the Ds - Ac cases. He finds that when an inhibitor (I), comparable to Ds , is adjacent to a Pg allele, a recessive pale green phenotype is produced. Removal of I

from *Pg*, which is brought about by the *En* factor thus paralleling the action of *Ac* on *Ds*, restores the normal activity of the *Pg* allele and green sectors appear on a pale green background.

Since *Ds* and *Ac* are inferred to consist of heterochromatin (this inference is largely based on the fact that *Dt* is in the terminal knob of the short arm of 9 and also by analogy with the variegated types of position effect in *Drosophila*) and since these loci control the time when certain genes become active—e.g., the activity of the *C* allele in the c^{m-1} complex is determined by *Ds* and *Ac*—McClintock (1951) suggests that elements in the heterochromatin regulate genic action in differentiation. Further discussion of this intriguing hypothesis lies beyond the scope of this review.

Although mutations have been induced in maize by ionizing radiations, ultraviolet, and chemical mutagens, we shall do no more than mention the conclusions from the extensive investigations of Stadler and his associates. When the mutagenic effect of X-rays was first discovered, it was generally accepted that true gene mutations were being induced. Stadler, however, concluded that X-radiation, although extremely effective in inducing heritable changes, did not produce mutations similar to those occurring spontaneously. This conclusion was reached after detailed studies with selected loci such as *A₁* and *R* which have favorable characteristics for mutation studies. An example of these studies is the work of Stadler and Roman (1948) who obtained 415 plants with changes at the *A₁* locus, involving the loss of *A₁* action, due to X-ray treatment. In only two of these plants was the pollen carrying the mutant *a₁* locus apparently normal in appearance. These two cases, designated *a-x1* and *a-x2*, and a third mutant, *a-x3*, with slightly subnormal pollen were carefully studied. All three were haplo-viable but had reduced transmission rates through the gametophyte generations. The *a-x1* mutant was normally transmitted through the female gametophyte in plants of *A/a-x1* constitution, but pollen with *a-x1* was only 50 per cent successful in competing with *A*-bearing pollen. Gametophytes with the *a-x2* mutant had 65 and 25 per cents of transmission through the female and male gametophytes, respectively, whereas the *a-x3* mutant was transmitted by only 21 per cent of the female gametophytes and by none of the male. All three homozygous types or any combination of the three gave lethal zygotes. Crossing over was reduced in adjacent regions in plants heterozygous for *a-x2* and *a-x3* but not in *a-x1* heterozygotes. The reduced transmission through the gametophytes, the recessive lethal effect, and the reduction in crossing over were all suggestive of deficiencies, but cytological examination of the long arm of chromosome 3 failed to disclose a visible

deficiency. However genetic tests proved that these three a_1 mutants were minute deficiencies including more than the loss of the A_1 gene. This was shown by the use of a ring chromosome possessing the A_1^b gene. Plants homozygous for the a - x mutants are lethal, but the ring chromosome carried chromatin covering the deficient segments of the a - x chromosomes; consequently plants with the ring and two a - x chromosomes were viable. Ring-bearing plants had a purple plant color owing to the presence of the A_1^b gene. The instability of the ring chromosome in somatic divisions gave rise to sectors with smaller rings deficient for various segments. When the A_1^b allele was lost, a brown-colored sector arose as expected. The presence of two other loci in the ring, missing from the a - x chromosomes, was indicated by the appearance of white sectors and of sectors which were inviable. Later, compelling evidence of the deficient nature of all three a - x mutants came from the finding that the sh_2 locus, which is only 0.25 map units to the right of A_1 , was missing from the a - x chromosomes.

Although the X-ray-induced mutants are not identical to those occurring spontaneously, Stadler (1941) found that some at least of the ultraviolet mutants could not be distinguished from spontaneous mutants. The nature of mutant changes induced by chemical mutagens remains to be ascertained.

The nature of spontaneous changes constitutes one of the most challenging problems, since they provide the ultimate source of genetic variation. In recent years an increasing amount of attention has been paid to the mutational characteristics of certain loci, especially those affecting endosperm characters. Mutation at the A_1 locus in chromosome 3 and at the R locus in chromosome 10 has been extensively studied. These loci offer the advantages of affecting anthocyanin formation of the aleurone, plant, and pericarp, of having a large series of alleles, some with nonlinear effects, and of providing a sufficient number of mutants for comparison. The A_1 locus has the further advantage of Laughnan's (1948, 1950) studies on the gene action, including dosage effect, competition, dominance relations, and pigment biosynthesis, of various alleles.

Although a considerable number of A alleles have arisen in experimental studies, only five have been found in different races of maize. The A allele present in nearly all North American strains produces anthocyanin in the aleurone and plant and a red pigment in the pericarp. The A^b allele isolated from an Ecuadorean race has a similar effect on aleurone and plant color but produces a dominant brown pericarp color. The a^p allele of South American extraction produces a pale aleurone color and a recessive red-brown plant color but has a

dominant brown pericarp effect similar to that of A^b . The a^b allele also from South American corn gives colorless aleurone and a recessive brown plant color but has a dominant brown pericarp effect. This allele was probably derived by mutation from a^p , since similar alleles have come from a^p in experimental cultures. The a allele, which is the lowest member of the series, is similar to a^b in effect on aleurone and plant color but has a recessive brown pericarp effect.

The A^b allele mutates to a new allele A^d which has the dominant brown pericarp action of A^b but whose pale aleurone and red-brown plant colors are recessive to those of A . Mutations of A^b to a^b have not been reported, but A^d mutants derived from A^b have given rise to a^b alleles. These A^d mutants, which occur with a frequency of about 1/1400, come from plants either homozygous or heterozygous for A^b . Laughnan (1949, 1952) found that 92 per cent of the mutations of A^b to A^d were associated with crossing over at the A^b locus. The A^b locus is compound; its two components, alpha and beta, are separable by crossing over. Localization of the point of crossing over to the A^b locus was possible, since all exchanges were between A^b and sh_2 , which lies only 0.25 map units to the right of A . The A^d mutants have only the alpha component; the complementary crossover class with the beta component has not been isolated, but there is reason to believe that it produces a purple aleurone and plant color effect, since the A^b allele, with both alpha and beta, has a level of pigmentation which can logically be ascribed to beta unless a position effect gives an unsuspected phenotype. The 8 per cent of exceptions where mutations of A^b to A^d occurred without detectable crossing over may result from crossing over between sister strands or from mutation of beta to a null form. Since mutations of A^b to A^d have occurred in heterozygotes where A^b was opposed by a deficiency, it is evident that mutation of A^b can take place without crossing over between nonsister chromatids. This does not, however, permit a decision between sister-strand crossing over and mutation of the beta component. Inasmuch as mutation of A^b to A^d occurs with approximately the same frequency in A^b/A^b as in A^b/a plants, those mutations involving the separation of alpha and beta are believed to be due to crossing over following oblique synapsis. Although the constitution of recessive a is uncertain with respect to units homologous to the alpha and beta components of A^b , Laughnan found that of 53 A^d mutants derived from A^b/a heterozygotes there were only three which were mutable with Dt , while the remaining 50 were stable with Dt . The mutable A^d 's have both the alpha component from A^b and recessive a ; it is the response of a to Dt which accounts for the appearance of deep-colored dots on the pale background produced by alpha. The stable A^d

mutants presumably lacked α . The disproportionate ratio of stable to mutable A^d 's is understandable if synapsis between α and the alpha component of A^b occurs more frequently than does pairing of α with beta, since only the latter kind of synapsis gives a crossover chromatid with both alpha and α (Fig. 25).

There are four main types of alleles at the R locus which are designated as R^r , R^g , r^r , and r^g . The R^r allele produces both aleurone and plant color, the R^g allele gives a colored aleurone but no plant color, the r^r allele produces colorless aleurone but a colored plant, while with the r^g allele no anthocyanin is found in either aleurone or plant. The component of the R gene affecting plant color was designated P and

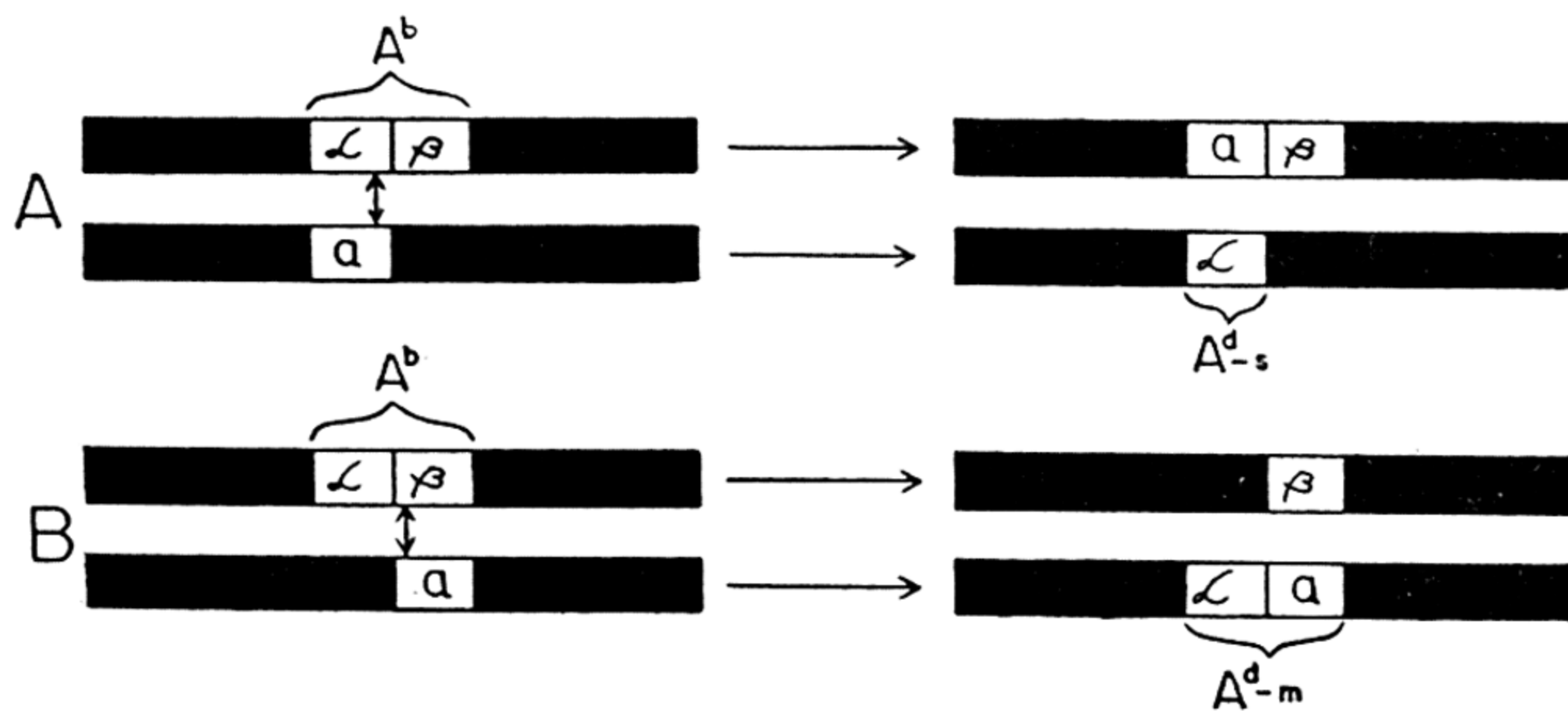


FIG. 25. Hypothetical schemes to account for the origin of (A) the A^d-s (stable) and (B) the A^d-m (mutable) derivatives following crossing over between nonsister strands in A^b/a individuals. (From Laughnan, 1952.)

that affecting the aleurone color, component S. Using this terminology the R^r allele is PS, the R^g allele is pS, the r^r allele is Ps, and the r^g allele is ps. The R^g allele is dominant to r^r for aleurone color but recessive for plant color—i.e., these alleles are nonlinear in their effects on different tissues. Stadler (1941, 1942, 1946, 1948, 1949, 1950, 1951) found that mutations occur in either the aleurone or plant color component but never, or rarely, did the same mutational event involve both the P and S components. Mutation of one component has no influence on the activity of the nonmutated component. One R^r allele might have a relatively high rate of P to p mutations but a low rate of S to s, or the reverse might be found for another allele. The mutation rates of the P and S components varied markedly in different strains, but this was shown to be largely due to modifying genes, some of which were placed in various chromosomes by linkage tests. The P and S components differed in their response to the same set of modifiers. The mutational behavior of the P and S components suggests that the R gene is compound, consisting of two independent units, one (P) determining plant color and the other (S) determining aleurone color.

That the R^r complex does consist of at least two genetic units, P and S, became evident when Stadler and Nuffer (1953) found that they were separable by crossing over. Crossing over between the P and S components yields recombination types which simulate gene mutations but which are distinguishable from them when genetic markers to the left and to the right of the R locus are employed. The discovery that in certain pS mutants, arising from PS, the apparent mutation of the P component to p markedly reduced the mutation rate of the S component was at first interpreted as indicating that the P and S components were not wholly independent. Recently, however, Stadler and Emmerling (1954) reported evidence that an R^g with a lowered mutation rate of the S component was deficient for the P component and was —S rather than pS in constitution. It is believed that crossover mutations of the R complex arise from unequal crossing over following synapsis of an S component with a P component. The failure to find one class of crossover mutations in PS/—S heterozygotes would be expected, since the kind of oblique synapsis essential for its occurrence could not take place. Recombination mutants are expected only from compound loci and are associated with meiotic crossing over. The majority of mutational changes at the R locus in most stocks are not connected with crossing over.

The A and R loci where alleles with nonlinear effects exist are both compound consisting of two, or more, separable genetic determiners with similar though not identical effects on pigment formation in different parts of the plant. These clusters of similar genetic units are believed to come from duplication followed by partial divergence in function through mutation.

The Dt -induced A alleles from recessive a provide valuable material for the study of spontaneous mutation. These A alleles, designate A' , yield mutation to a (called a'). Mutation of the A' alleles may be induced by Dt , but this is uncertain (Stadler, 1951). These a' mutants differ markedly in their response to Dt . Many of the a' mutants from A' were much more mutable with Dt than was the original a gene from which the A' alleles were derived. Since these a' mutants frequently give rise to new A alleles (A''), which in turn will mutate back to a'' alleles, it is possible by this mutational cycle to obtain a large number of mutant genes, all descendants from one a allele, and by a comparison of the effects and behavior of these mutants to arrive at some understanding of the mutational potentialities of this locus.

REFERENCES

- ANDERSON, E. G. 1925. Crossing over in a case of attached X chromosomes in *Drosophila melanogaster*. *Genetics* 10: 403–417.

- ANDERSON, E. G. 1936. Induced chromosomal alterations in maize. "Biological Effects of Radiation," Vol. I, pp. 297-1310, McGraw-Hill, New York.
- ANDERSON, E. G., and RANDOLPH, L. F. 1945. Location of the centromere on the linkage maps of maize. *Genetics* **30**: 518-526.
- BARCLAY, P. 1954. Relation between Activator (*Ac*) and Modulator (*Mp*). *Maize Genetics Coop. News Letter* **28**: 77.
- BEADLE, G. W. 1930. Genetical and cytological studies of Mendelian asynapsis in *Zea mays*. *Cornell Univ. Agr. Expt. Sta. Mem.* **129**: 1-23.
- BEADLE, G. W. 1931. A gene in maize for supernumerary cell divisions following meiosis. *Cornell Univ. Agr. Expt. Sta. Mem.* **135**: 1-12.
- BEADLE, G. W. 1932a. The relation of crossing over to chromosome association in *Zea-Euchlaena* hybrids. *Genetics* **17**: 481-501.
- BEADLE, G. W. 1932b. A possible influence of the spindle fiber on crossing over in *Drosophila*. *Proc. Natl. Acad. Sci. U. S.* **18**: 160-165.
- BEADLE, G. W. 1932c. A gene for sticky chromosomes in *Zea mays*. *Z. ind. Abstamm.-u. Verebungsl.* **63**: 195-217.
- BEADLE, G. W. 1932d. A gene in *Zea mays* for the failure of cytokinesis during meiosis. *Cytologia (Tokyo)* **3**: 142-155.
- BEADLE, G. W. 1933. Further studies of asynaptic maize. *Cytologia (Tokyo)* **4**: 269-287.
- BEADLE, G. W. 1937. Chromosome aberration and gene mutation in sticky chromosome plants of *Zea mays*. *Cytologia (Tokyo)* (Fujii Jubilee Volume), pp. 43-56.
- BEADLE, G. W., and EMERSON, S. 1935. Further studies of crossing over in attached X chromosomes in *Drosophila melanogaster*. *Genetics* **20**: 192-206.
- BRIDGES, C. B. 1916. Non-disjunction as proof of the chromosome theory of heredity. *Genetics* **1**: 1-52, 107-163.
- BRIDGES, C. B., and ANDERSON, E. G. 1925. Crossing over in the X chromosomes of triploid females of *Drosophila melanogaster*. *Genetics* **10**: 418-441.
- BRINK, R. A. 1927. The occurrence of semi-sterility in maize. *J. Heredity* **18**: 266-270.
- BRINK, R. A. 1954a. The analysis of a twin mutation of medium variegated pericarp. *Maize Genetics Coop. News Letter* **28**: 77-78.
- BRINK, R. A. 1954b. Reduplication of transposed Modulator in a variegated pericarp strain. *Maize Genetics Coop. News Letter* **28**: 78-79.
- BRINK, R. A., and BURNHAM, C. R. 1929. Inheritance of semi-sterility in maize. *Am. Naturalist* **63**: 301-316.
- BRINK, R. A., and COOPER, D. C. 1935. A proof that crossing over involves an exchange of segments between homologous chromosomes. *Genetics* **20**: 22-35.
- BRINK, R. A., and NILAN, R. A. 1952. The relation between light variegated and medium variegated pericarp in maize. *Genetics* **37**: 519-544.
- BROWN, W. L. 1949. Numbers and distribution of chromosome knobs in United States maize. *Genetics* **34**: 524-536.
- BURNHAM, C. R. 1930. Genetical and cytological studies of semi-sterility and related phenomena in maize. *Proc. Natl. Acad. Sci. U. S.* **16**: 269-277.
- BURNHAM, C. R. 1932a. An interchange in maize giving low sterility and chain configurations. *Proc. Natl. Acad. Sci. U. S.* **18**: 434-440.
- BURNHAM, C. R. 1932b. The association of non-homologous parts in chromosomal interchange in maize. *Proc. 6th Intern. Congr. Genet.* **2**: 19-20.
- BURNHAM, C. R. 1934. Chromosomal interchanges in maize: Reduction of crossing-over and the association of non-homologous parts. *Am. Naturalist* **68**: 81-82.

- BURNHAM, C. R. 1949. Chromosome segregation in maize translocations in relation to crossing over in interstitial segments. *Proc. Natl. Acad. Sci. U. S.* **35**: 349-356.
- BURNHAM, C. R. 1950. Chromosome segregation in translocations involving chromosome 6 in maize. *Genetics* **35**: 446-481.
- BURNHAM, C. R., and CARTLEDGE, J. L. 1939. Linkage relations between smut resistance and semisterility in maize. *J. Am. Soc. Agron.* **31**: 924-933.
- CHASE, S. S. 1949. Monoploid frequencies in a commercial double cross hybrid maize, and in its component single cross hybrids and inbred lines. *Genetics* **34**: 328-332.
- CHASE, S. S. 1951. The monoploid method of developing inbred lines. *Proc. 6th Ann. Hybrid Corn Industry-Research Conf.* **6**: 29-34.
- CLARK, F. J. 1940. Cytogenetic studies of divergent meiotic spindle formation in *Zea mays*. *Am. J. Botany* **27**: 547-559.
- CLARK, F. J. 1942. Cytological and genetic studies of sterility in inbreds of similar and diverse genetic origin. *Connecticut Agr. Expt. Sta. Bull.* **465**: 705-726.
- CLARKE, A. E., and ANDERSON, E. G. 1935. A chromosomal interchange in maize without ring formation. *Am. J. Botany* **22**: 711-716.
- CLEVELAND, L. R. 1949. The whole life cycle of chromosomes and their coiling systems. *Trans. Am. Phil. Soc.* **39**: 1-100.
- COLLINS, G. N., and KEMPTON, J. H. 1927. Variability in the linkage of two seed characters in maize. *U. S. Dept. Agr. Bull.* **1468**.
- COOPER, D. C. 1952. The transfer of desoxyribose nucleic acid from the tapetum to the microsporocytes at the onset of meiosis. *Am. Naturalist* **86**: 219-230.
- COOPER, D. C., and BRINK, R. A. 1937. Chromosome homology in races of maize from different geographical regions. *Am. Naturalist* **71**: 582-587.
- COOPER, K. W. 1945. Normal segregation without chiasmata in female *Drosophila melanogaster*. *Genetics* **30**: 472-484.
- CREIGHTON, H. B. 1934. Three cases of deficiency in chromosome 9 of *Zea mays*. *Proc. Natl. Acad. Sci. U. S.* **20**: 111-115.
- CREIGHTON, H. B., and MCCLINTOCK, B. 1931. A correlation of cytological and genetical crossing-over in *Zea mays*. *Proc. Natl. Acad. Sci. U. S.* **17**: 492-497.
- CREIGHTON, H. B., and MCCLINTOCK, B. 1932. Cytological evidence for 4-strand crossing over in *Zea mays*. *Proc. 6th Intern. Congr. Genet.* **2**: 392.
- CREIGHTON, H. B., and MCCLINTOCK, B. 1935. The correlation of cytological and genetical crossing-over in *Zea mays*. A corroboration. *Proc. Natl. Acad. Sci. U. S.* **21**: 148-150.
- DARLINGTON, C. D. 1934. The origin and behaviour of chiasmata. VII. *Zea mays*. *Z. ind. Abstamm.-u. Vererbungslehre* **67**: 96-114.
- DARLINGTON, C. D., and UPCOTT, M. B. 1941. The activity of inert chromosomes in *Zea mays*. *J. Genet.* **41**: 275-296.
- DOBZHANSKY, TH., and RHOADES, M. M. 1938. A possible method for locating favorable genes in maize. *J. Am. Soc. Agron.* **30**: 668-675.
- EINSET, J. 1943. Chromosome length in relation to transmission frequency of maize trisomes. *Genetics* **28**: 349-364.
- EMERSON, R. A. 1914. Inheritance of a recurring somatic variation in variegated ears of maize. *Am. Naturalist* **48**: 87-115.
- EMERSON, R. A. 1917. Genetical studies on variegated pericarp in maize. *Genetics* **2**: 1-35.
- EMERSON, R. A. 1929. Frequency of somatic mutation in variegated pericarp of maize. *Genetics* **14**: 488-511.

- EMERSON, R. A., and HUTCHINSON, C. B. 1921. The relative frequency of crossing over in microspore and in megaspore development in maize. *Genetics* 6: 417-432.
- EMERSON, R. A., and RHOADES, M. M. 1933. Relation of chromatid crossing over to the upper limit of recombination percentages. *Am. Naturalist* 67: 1-4.
- EMERSON, S., and BEADLE, G. W. 1933. Crossing-over near the spindle fiber in attached-X chromosomes of *Drosophila melanogaster*. *Z. ind. Abstamm.-u. Vererbungslehre* 65: 129-140.
- EYSTER, W. H. 1921. The linkage relations between the factors for tunicate ear and starchy-sugary endosperm in maize. *Genetics* 6: 209-240.
- EYSTER, W. H. 1922. The intensity of linkage between the factors for sugary endosperm and for tunicate ears, and the relative frequency of their crossing over in microspore and megaspore development. *Genetics* 7: 597-601.
- FISK, E. L. 1925. The chromosomes of *Zea mays*. *Proc. Natl. Acad. Sci. U. S.* 11: 352-356.
- FISK, E. L. 1927. The chromosomes of *Zea mays*. *Am. J. Botany* 14: 54-75.
- FREEMAN, W. H. 1946. The inheritance of husk length, ear length, and days to silking in maize. Annual Meeting of The American Society of Agronomy, Feb. 27-March 1, Crop Div. Program, pp. 7-8.
- GILES, N. H., JR. 1943. A pericentric inversion in *Gasteria* resulting in apparent iso-chromosomes at meiosis. *Proc. Natl. Acad. Sci. U. S.* 30: 1-5.
- GILLES, A., and RANDOLPH, L. F. 1951. Reduction of quadrivalent frequency in autotetraploid maize during a period of 10 years. *Am. J. Botany* 38: 12-17.
- JENNINGS, H. S. 1923. The numerical relations in the crossing over of the genes, with a critical examination of the theory that the genes are arranged in a linear series. *Genetics* 8: 393-457.
- KIESSELBACH, T. A., and PETERSON, N. F. 1925. The chromosome number of maize. *Genetics* 10: 80-85.
- KUWADA, Y. 1911. Meiosis in the pollen mother cells of *Zea mays*. *Botan. Mag. (Tokyo)* 25: 163-181.
- KUWADA, Y. 1915. Ueber die Chromosomenzahl von *Zea mays*. *Botan. Mag. (Tokyo)* 29: 83-89.
- KUWADA, Y. 1919. Die Chromosomenzahl von *Zea mays*. Ein Beitrag zur Hypothese der Individualitat der Chromosomen und zur Frage uber die Herkunft von *Zea mays*. *J. Coll. Sci. Imperial Univ. Tokyo* 39: 1-48.
- KUWADA, Y. 1925. On the number of chromosomes in maize. *Botan. Mag. (Tokyo)* 39: 227-234.
- LAUGHNAN, J. R. 1948. The action of allelic forms of the gene *A* in maize. I. Studies of variability, dosage and dominance relations. The divergent character of the series. *Genetics* 33: 488-517.
- LAUGHNAN, J. R. 1949. The action of allelic forms of the gene *A* in maize. II. The relation of crossing over to mutation of *A^b*. *Proc. Natl. Acad. Sci. U. S.* 35: 167-178.
- LAUGHNAN, J. R. 1950. The action of allelic forms of the gene *A* in maize. III. Studies on the occurrence of isoquercitrin in brown and purple plants and its lack of identity with the brown pigments. *Proc. Natl. Acad. Sci. U. S.* 36: 312-318.
- LAUGHNAN, J. R. 1952. The action of allelic forms of the gene *A* in maize. IV. On the compound nature of *A^b* and the occurrence and action of its *A^d* derivatives. *Genetics* 37: 375-395.
- LAUGHNAN, J. R., and COE, E. H. 1953. A-B interchanges as a method of screening for new mutants in specific segments. *Maize Genetics Coop. News Letter* 27: 55-56.

- LONGLEY, A. E. 1924. Chromosomes in maize and maize relatives. *J. Agr. Research* **28**: 673-681.
- LONGLEY, A. E. 1927. Supernumerary chromosomes in *Zea mays*. *J. Agr. Research* **35**: 769-784.
- LONGLEY, A. E. 1937. Morphological characters of Teosinte chromosomes. *J. Agr. Research* **54**: 835-862.
- LONGLEY, A. E. 1938. Chromosomes of maize from North American Indians. *J. Agr. Research* **56**: 177-196.
- LONGLEY, A. E. 1939. Knob positions on corn chromosomes. *J. Agr. Research* **59**: 475-490.
- LONGLEY, A. E. 1945. Abnormal segregation during megasporogenesis in maize. *Genetics* **30**: 100-113.
- LONGLEY, A. E. 1950. Cytological analysis of translocations in corn chromosomes resulting from ionizing radiation of the test Able Atomic Bomb and X-rays and of translocations from other sources. Report of Naval Medical Research Section, Joint Task Force One, on Biological Aspects of Atomic Bomb Tests. Appendix No. 10, pp. 1-60.
- MANGELSDORF, P. C., and CAMERON, J. W. 1942. Western Guatemala a secondary center of origin of cultivated maize varieties. *Botan. Museum Leaflets Harvard Univ.* **10**: 217-252.
- MANGELSDORF, P. C., and REEVES, R. G. 1939. The origin of Indian corn and its relatives. *Texas Agr. Expt. Sta. Bull.* **574**: 1-315.
- MANN, T. J. 1950. Locating genetic factors for kernel-row number by use of translocations. *Maize Genetics Coop. News Letter* **24**: 22.
- MCCCLINTOCK, B. 1929a. Chromosome morphology in *Zea mays*. *Science* **69**: 629.
- MCCCLINTOCK, B. 1929b. A cytological and genetical study of triploid maize. *Genetics* **14**: 180-222.
- MCCCLINTOCK, B. 1930. A cytological demonstration of the location of an interchange between two non-homologous chromosomes of *Zea mays*. *Proc. Natl. Acad. Sci. U. S.* **16**: 791-796.
- MCCCLINTOCK, B. 1931. Cytological observations of deficiencies involving known genes, translocations, and an inversion in *Zea mays*. *Missouri Agr. Expt. Sta. Research Bull.* **163**: 1-30.
- MCCCLINTOCK, B. 1932. A correlation of ring-shaped chromosomes with variegation in *Zea mays*. *Proc. Natl. Acad. Sci. U. S.* **18**: 677-681.
- MCCCLINTOCK, B. 1933. The association of non-homologous parts of chromosomes in the mid-prophase of meiosis in *Zea mays*. *Z. Zellforsch. u. mikroskop. Anat.* **19**: 191-237.
- MCCCLINTOCK, B. 1934. The relation of a particular chromosomal element to the development of the nucleoli in *Zea mays*. *Z. Zellforsch. u. mikroskop. Anat.* **21**: 294-328.
- MCCCLINTOCK, B. 1938a. The fusion of broken ends of sister half-chromatids following chromatid breakage at meiotic anaphases. *Missouri Agr. Expt. Sta. Research Bull.* **290**: 1-48.
- MCCCLINTOCK, B. 1938b. The production of homozygous deficient tissues with mutant characteristics by means of the aberrant mitotic behavior of ring-shaped chromosomes. *Genetics* **23**: 315-376.
- MCCCLINTOCK, B. 1939. The behavior in successive nuclear divisions of a chromosome broken at meiosis. *Proc. Natl. Acad. Sci. U. S.* **25**: 405-416.
- MCCCLINTOCK, B. 1941a. The association of mutants with homozygous deficiencies in *Zea mays*. *Genetics* **26**: 542-571.

- McCLINTOCK, B. 1941b. The stability of broken ends of chromosomes in *Zea mays*. *Genetics* **26**: 234–282.
- McCLINTOCK, B. 1943. Maize genetics. *Yearbook Carnegie Inst.* **42**: 148–152.
- McCLINTOCK, B. 1944. The relation of homozygous deficiencies to mutations and allelic series in maize. *Genetics* **29**: 478–502.
- McCLINTOCK, B. 1945. Neurospora. I. Preliminary observations of the chromosomes of *Neurospora crassa*. *Am. J. Botany* **32**: 671–678.
- McCLINTOCK, B. 1950. The origin and behavior of mutable loci in maize. *Proc. Natl. Acad. Sci. U. S.* **36**: 344–355.
- McCLINTOCK, B. 1951. Chromosome organization and genic expression. *Cold Spring Harbor Symposia Quant. Biol.* **16**: 13–47.
- McCLINTOCK, B., and HILL, H. E. 1931. The cytological identification of the chromosome associated with the R-G linkage group in *Zea mays*. *Genetics* **16**: 175–190.
- MORGAN, D. T., JR. 1943. The formation of chromocenters in interkinetic nuclei of maize. *J. Heredity* **34**: 194–198.
- MORGAN, D. T., JR. 1950. Cytogenetic study of inversions in *Zea mays*. *Genetics* **35**: 153–174.
- O'MARA, J. G. 1942. A cytogenetic study of *Zea* and *Euchlaena*. *Missouri Agr. Expt. Sta. Bull.* **341**: 3–16.
- OSTERGREN, G. 1945. Parasitic nature of extra fragment chromosomes. *Botan. Notiser* **1945**, Hefte **2**: 157–163.
- PATTERSON, E. B. 1952. The use of functional duplicate-deficient gametes in locating genes in maize. *Genetics* **37**: 612.
- PETERSON, P. A. 1953. A mutable pale green locus in maize. *Records Genetics Soc. Amer.* **22**: 92–93.
- RANDOLPH, L. F. 1928a. Chromosome numbers in *Zea mays* L. *Cornell Univ. Agr. Expt. Sta. Mem.* **117**.
- RANDOLPH, L. F. 1928b. Types of supernumerary chromosomes in maize. *Anat. Record* **41**: 102.
- RANDOLPH, L. F. 1932. Some effects of high temperature on polyploidy and other variations in maize. *Proc. Natl. Acad. Sci. U. S.* **18**: 222–229.
- RANDOLPH, L. F. 1935. Cytogenetics of tetraploid maize. *J. Agr. Research* **50**: 591–605.
- RANDOLPH, L. F. 1941. Genetic characteristics of the B-chromosomes in maize. *Genetics* **26**: 608–631.
- RANDOLPH, L. F. 1952. New evidence on the origin of maize. *Am. Naturalist* **86**: 193–202.
- RANDOLPH, L. F., and FISCHER, H. E. 1939. The occurrence of parthenogenetic diploids in tetraploid maize. *Proc. Natl. Acad. Sci. U. S.* **25**: 161–164.
- RANDOLPH, L. F., and HAND, D. B. 1940. Relation between carotenoid content and number of genes per cell in diploid and tetraploid corn. *J. Agr. Research* **60**: 51–64.
- REEVES, R. G. 1925. Chromosome studies of *Zea mays*. *Proc. Iowa Acad. Sci.* **22**: 171–179.
- RHOADES, M. M. 1933a. An experimental and theoretical study of chromatid crossing over. *Genetics* **18**: 535–555.
- RHOADES, M. M. 1933b. A secondary trisome in maize. *Proc. Natl. Acad. Sci. U. S.* **19**: 1031–1038.
- RHOADES, M. M. 1936a. Note on the origin of triploidy in maize. *J. Genet.* **33**: 355–357.

- RHOADES, M. M. 1936b. A cytogenetic study of a chromosome fragment in maize. *Genetics* **21**: 491-502.
- RHOADES, M. M. 1938. Effect of the *Dt* gene on the mutability of the a_1 allele in maize. *Genetics* **23**: 377-395.
- RHOADES, M. M. 1940. Studies of a telocentric chromosome in maize with reference to the stability of its centromere. *Genetics* **25**: 483-520.
- RHOADES, M. M. 1941a. Different rates of crossing over in male and female gametes of maize. *J. Am. Soc. Agron.* **33**: 603-615.
- RHOADES, M. M. 1941b. The genetic control of mutability in maize. *Cold Spring Harbor Symposia Quant. Biol.* **9**: 138-144.
- RHOADES, M. M. 1942. Preferential segregation in maize. *Genetics* **27**: 395-407.
- RHOADES, M. M. 1945. On the genetic control of mutability in maize. *Proc. Natl. Acad. Sci. U. S.* **31**: 91-95.
- RHOADES, M. M. 1950. Meiosis in maize. *J. Heredity* **41**: 58-67.
- RHOADES, M. M. 1952. Preferential segregation in maize. In "Heterosis," Chapter 4, pp. 66-80. Iowa State College Press, Ames.
- RHOADES, M. M., and DEMPSEY, E. 1953. Cytogenetic studies of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. *Am. J. Botany* **40**: 405-424.
- RHOADES, M. M., and McCLINTOCK, B. 1935. The cytogenetics of maize. *Botan. Rev.* **1**: 292-325.
- RHOADES, M. M., and RHOADES, V. H. 1939. Genetic studies with factors in the tenth chromosome in maize. *Genetics* **24**: 302-314.
- RHOADES, M. M., and VILKOMERSON, H. 1942. On the anaphase movement of chromosomes. *Proc. Natl. Acad. Sci. U. S.* **28**: 433-436.
- RHOADES, V. H. 1935. The location of a gene for disease resistance in maize. *Proc. Natl. Acad. Sci. U. S.* **21**: 243-246.
- ROMAN, H. 1947. Mitotic nondisjunction in the case of interchanges involving the B-type chromosome in maize. *Genetics* **32**: 391-409.
- ROMAN, H. 1948a. Directed fertilization in maize. *Proc. Natl. Acad. Sci. U. S.* **34**: 36-42.
- ROMAN, H. 1948b. Selective fertilization in maize. *Genetics* **33**: 122.
- ROMAN, H. 1949. Factors affecting mitotic nondisjunction in maize. *Records Genetics Soc. Amer.* **18**: 112.
- ROMAN, H., and ULLSTRUP, A. J. 1951. The use of A-B translocations to locate genes in maize. *Agron. J.* **43**: 450-454.
- RUSSELL, W. A. and BURNHAM, C. R. 1950. Cytogenetic studies of an inversion in maize. *Sci. Agr.* **30**: 93-111.
- SABOE, L. C., and HAYES, H. K. 1941. Genetic studies of reactions to smut and firing in maize by means of chromosomal translocations. *J. Am. Soc. Agron.* **33**: 463-470.
- SCHWARTZ, D. 1953a. The behavior of an X-ray-induced ring chromosome in maize. *Am. Naturalist* **87**: 19-28.
- SCHWARTZ, D. 1953b. Studies on the mechanism of crossing over. *Records Genetics Soc. Amer.* **22**: 99-100.
- SCHWARTZ, D. 1953c. Evidence for sister-strand crossing over in maize. *Genetics* **38**: 251-260.
- SCHWARTZ, D. 1954. Studies on the mechanism of crossing over. *Genetics* **39**: 692-700.
- SINGLETON, W. R. 1939. Cytological observations on deficiencies produced by treating maize pollen with ultraviolet light. *Genetics* **24**: 109.

- SPRAGUE, G. F. 1932a. The nature and extent of hetero-fertilization in maize. *Genetics* **17**: 358-368.
- SPRAGUE, G. F. 1932b. The inheritance of colored scutellums in maize. *U. S. Dept. Agr. Tech. Bull.* **292**: 1-43.
- SPRAGUE, G. F. 1941. The location of dominant favorable genes in maize by means of an inversion. *Genetics* **26**: 170.
- STADLER, L. J. 1926. Variability of crossing over in maize. *Genetics* **11**: 1-37.
- STADLER, L. J. 1933. On the genetic nature of induced mutations in plants. II. A haplo-viable deficiency in maize. *Missouri Agr. Expt. Sta. Research Bull.* **204**: 1-29.
- STADLER, L. J. 1935. Genetic behaviour of a haplo-viable internal deficiency in maize. *Am. Naturalist* **69**: 80-81.
- STADLER, L. J. 1941. The comparison of ultra-violet and X-ray effects on mutation. *Cold Spring Harbor Symposia Quant. Biol.* **9**: 168-177.
- STADLER, L. J. 1942. Some observations on gene variability and spontaneous mutation. The Spragg Memorial Lectures (Third Series), Michigan State College.
- STADLER, L. J. 1946. Spontaneous mutation at the *R* locus in maize. I. The aleurone-color and plant-color effects. *Genetics* **31**: 377-394.
- STADLER, L. J. 1948. Spontaneous mutation at the *R* locus in maize. II. Race differences in mutation rate. *Am. Naturalist* **82**: 289-314.
- STADLER, L. J. 1949. Spontaneous mutation at the *R* locus in maize. III. Genetic modifiers of mutation rate. *Am. Naturalist* **83**: 5-30.
- STADLER, L. J. 1950. Spontaneous mutation at the *R* locus in maize. IV. An *R* linked modifier of *R* mutation rate. *Portugaliae Acta Biol. Ser. A*, Goldschmidt vol., pp. 785-797.
- STADLER, L. J. 1951. Spontaneous mutation in maize. *Cold Spring Harbor Symposia Quant. Biol.* **16**: 49-63.
- STADLER, L. J., and EMMERLING, M. 1954. Problems of gene structure. III. Relationship of unequal crossing-over to the interdependence of *R'* Elements (S) and (P). *Science* **119**: 585.
- STADLER, L. J., and NUFFER, M. G. 1953. Problems of gene structure. II. Separation of *R'* elements (S) and (P) by unequal crossing over. *Science* **117**: 471-472.
- STADLER, L. J., and ROMAN, H. 1948. The effect of X-rays upon mutation of the gene *A* in maize. *Genetics* **33**: 273-303.
- STERN, C. 1931. Zytologisch-genetische Untersuchungen als Beweise fur die Morgansche Theorie des Faktorenaustauschs. *Biol. Zentr.* **51**: 547-587.
- STURTEVANT, A. H. 1931. Known and probable inverted sections of the autosomes of *Drosophila melanogaster*. *Carnegie Inst. Wash. Publ.* **421**: 1-27.
- STURTEVANT, A. H., and BEADLE, G. W. 1936. The relations of inversions in the X chromosome of *Drosophila melanogaster* to crossing over and disjunction. *Genetics* **21**: 554-604.
- SUTO, T. 1952. Genetic analysis of a mosaic pericarp in maize, with special reference to the genic change of the color pattern induced by the possibly unequal crossing-over in a small region containing the *P* locus and its neighbors of chromosome 1. *J. Fac. Sci. Hokkaido Univ. (Series V)* **6**: 68-150.
- WEIJER, J. 1952. A catalogue of genetic maize types together with a maize bibliography. *Bibliographia Genetica* **14**: 189-425.

CHAPTER V

Corn Breeding

G. F. SPRAGUE

I. Introduction

Corn breeding has passed through several distinct phases during its recorded history. Data accumulated during the earlier portion of this period are of limited interest except as they supply background information which may be useful in the interpretation of current corn-breeding

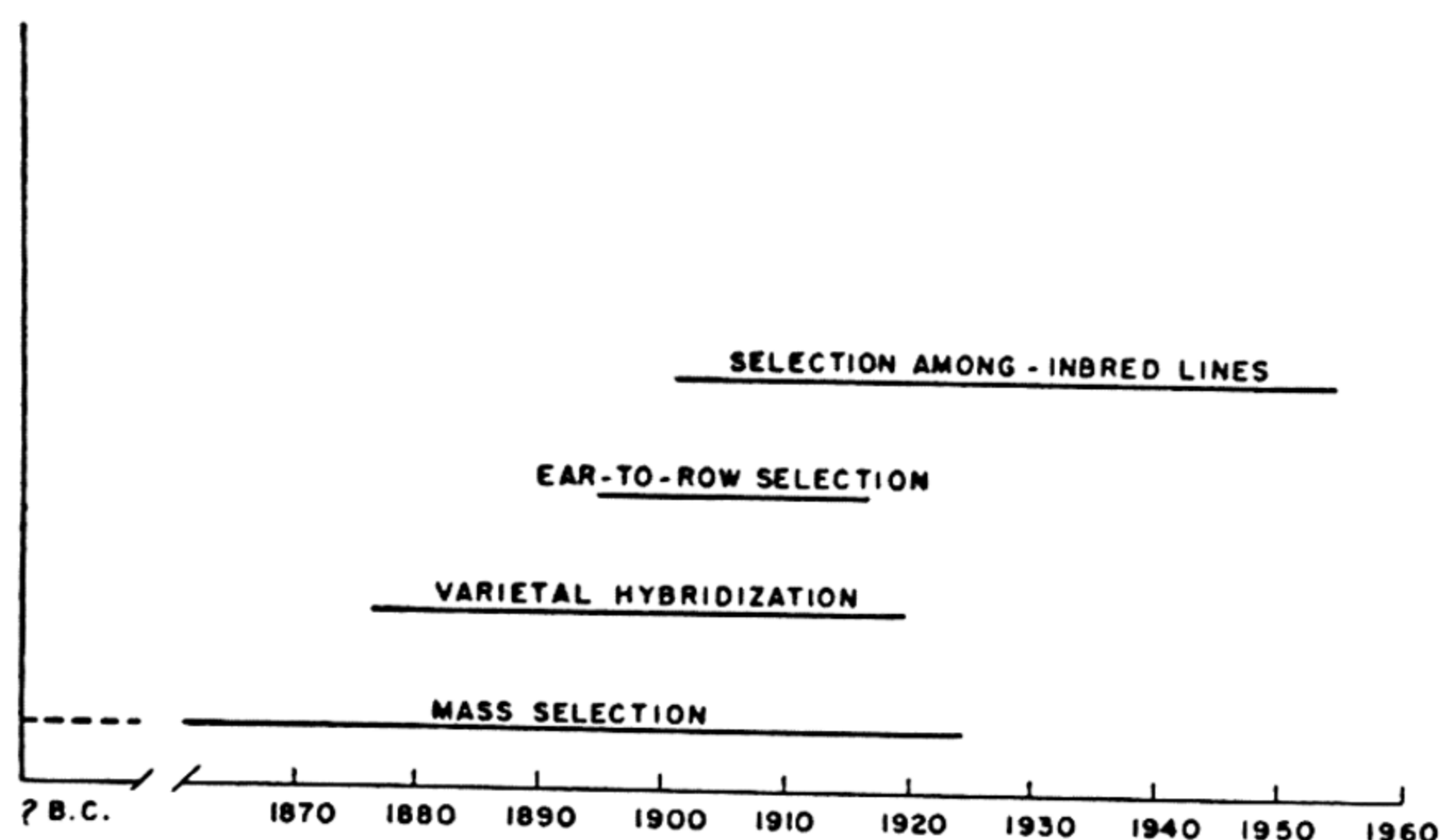


FIG. 1. A schematic representation of the time sequence of the more commonly used maize-breeding methods.

methods. An attempt has been made to illustrate the time sequence of the several breeding methods by the illustration presented in Fig. 1.

II. Mass Selection

Mass selection for the improvement of corn undoubtedly had its inception with the beginning of domestication of the corn plant. Since the harvesting of each ear is a separate operation, any variation in ear size would be readily apparent, and it would be quite logical for the larger and more desirable ears to be retained for seed.

Actually mass selection in corn, as practiced, never progressed much beyond this stage. Individual ears were chosen on the basis of plant and ear characteristics. These selected ears were composited and the bulked

seed used for planting the following season. The practice of compositing seed precluded any information on progeny performance. The lack of information on male parentage, progeny performance, and the confusing effects of soil variability on the phenotype of the plants selected would all operate to reduce the efficiency of the selection practiced.

Critical information on the effectiveness of mass selection is almost completely lacking. The wide range in plant and ear characteristics among recognized corn varieties strongly suggests that mass selection was reasonably effective. Unfortunately relatively little is known as to the time involved in producing these characteristic differences. The time requirements naturally would differ depending upon the genetic complexity of the attribute undergoing selection. One illustration indicating that changes in certain attributes may have been relatively rapid is presented in a letter by Mr. H. E. Bidwell of Minnesota to the editor of the *Agricultural Annual* and published in 1868. A part of the letter is quoted as follows:

A man in Tennessee gave me a good idea which I think worth publishing. He said, "Five years ago my corn yielded but one ear to each stalk, on an average, although I had long practiced selecting my seed corn from stalks bearing two ears. It occurred to me that the ears on the two-eared stalks were fertilized by adjoining plants bearing one ear only. I therefore resolved to raise my seed corn by itself, giving it the best of soil and culture, and before the silks appeared, breaking off the male flowers (tassels or spindles) from those having but one ear. You see the results—entire fields bearing nearly uniformly two ears to the stalk."

The selection reported here would be expected to be somewhat more effective than the mass selection normally practiced since it involved a greater than average control of the male parent.

Data on the effectiveness of mass selection for several ear characters are presented by Williams and Welton (1915). The results from one of these experiments involving selection for ear length in the variety CLARAGE are presented in Table I. A casual examination of these data indicates that the selection for ear length was not effective in separating the original population into two distinct groups, nor did the selection have any important effect on yield. However, before one concludes that mass selection was ineffective several aspects of the experimental design should be considered. Some of the factors which undoubtedly contributed to the ineffectiveness of the selection practiced were:

1. Small selection differential. The average difference in ear length for the two contrasting types was only 2.49 inches. Neither long nor short ears were selected unless they conformed to corn show standards. The effect of environment on phenotype would operate to further reduce the selection differential.

2. Lack of parentage control. The contrasting selections were grown in adjacent plots to increase the accuracy of yield comparisons. This method of planting would facilitate interpollination between the two groups, which would favor the regression of ear length toward that characteristic of the original population mean.

The data available do not provide any measure of the importance of these two factors. It appears, however, that these two forces might be sufficiently important to mask the effects of the selection practiced.

TABLE I

THE EFFECT OF SELECTION FOR LONG AND SHORT EARS IN THE VARIETY CLARAGE^a

Year	Yield, bushels per acre			Length of ears in inches					
	Shelled corn			Seed			Crop		
	Long	Short	Diff.	Long	Short	Diff.	Long	Short	Diff.
1907	64.95	65.38	-0.43	9.43	7.11	2.32	7.56	7.12	0.44
1908	68.22	67.77	+0.45	—	—	—	—	—	—
1909	85.49	82.58	+2.91	8.90	6.60	2.30	7.92	6.87	1.05
1910	31.03	36.74	-5.71	9.50	6.90	2.60	6.25	5.58	0.67
1911	64.81	69.28	-4.47	8.50	6.20	2.30	6.85	6.51	0.34
1912	62.13	55.90	+6.23	8.90	6.60	2.30	7.20	6.28	0.92
1913	68.96	63.61	+5.35	8.90	6.30	2.60	7.58	6.29	1.29
1914	61.68	62.29	-0.61	9.10	6.10	3.00	—	—	—
8 yr.	63.41	62.94	+0.47	9.03	6.54	2.49	7.23	6.44	0.78

^a Taken from Table XV Corn Experiments. *Ohio Agr. Expt. Sta. Bull.* **282**, 1915.

Data on the effectiveness of mass selection for yielding ability are almost completely lacking. Hull (1945, 1952) infers from this that the genes contributing to the additive portion of the genetic variance had become fixed and therefore further improvement by mass selection was impossible. This does not appear to be a necessary conclusion. There is a large body of indirect evidence that selection may have been effective in modifying yield of grain.

If one examines the data on corn yield trials published by experiment stations during the period from about 1860 to 1900, it will be noted that many varieties were included for only a short period of years and then discarded because of poor yielding ability. Varieties such as REID did not come into prominence until after winning at the Illinois State Fair at Peoria in 1891 and the World Columbian Exposition in 1893. This variety is reported to have had its origin as a varietal hybrid made in 1847. During the period from 1890 to 1920 this variety became very

widely distributed, and local strains were developed by numerous breeders and corn show enthusiasts. The Iowa State Corn Yield test was established in 1920 and in the testing of strains adapted to Iowa large differences in yielding ability among the various REID substrains were demonstrated. In the report of the corn yield test for 1920 sponsored by the Iowa Corn and Small Grain Growers Association, Professor H. D. Hughes then in charge of the Farm Crops Section was quoted as follows:

There are hundreds of strains of Reid's Yellow Dent Corn in Iowa and there is as much difference in the yielding power of different strains of this one variety as between distinct varieties.

In the unpublished data of the Iowa Corn Yield test for 1923, 21 open-pollinated varieties were included in the south central and 30 varieties in the southern section. The number of REID yellow dent entries in these two sections were 13 and 17, respectively. In the south central section yields of the REID entries ranged from 66.06 to 55.84 and in the southern section, from 63.84 to 56.35 bu. per acre. These data are from the sectional summaries based on a minimum of five replications at each of three locations. No standard errors were calculated for these tests, but the variation among means was sufficiently great to suggest that real differences in yielding ability were involved.

However it would not be logical to attribute all of the observed differences in yields to the mass selection practiced in isolating the strain. Accidental hybridization, leading to increased genetic variability, cannot be ruled out as a possible factor contributing to the observed strain differences. However, there appears to be little justification for the assumption that mass selection was not one of the causal factors involved. Data to be presented in a later section provide an independent and convincing demonstration that at least one open-pollinated variety (KRUG) is still heterozygous for an appreciable number of genetic factors contributing to the additive genetic variance.

The corn shows played a dominant role in the recognition and distribution of varieties during the period from about 1890 to 1920. A score card for judging corn was prepared by Orange Judd for the Illinois State Fair of 1891. The distribution of a corn variety was largely dependent upon winning at a local, state, or national show. Prize-winning single- or ten-ear samples often sold for considerable sums. Gradually it came to be appreciated that a winning sample was a measure of the showman's ability and patience in sorting over a large volume of ears to find a sample corresponding to the show card ideal rather than a measure of the breeding worth of the particular sample.

As this idea grew, large numbers of experiments were conducted to measure the relationship between various ear and kernel characteristics and yielding ability. These experiments have been summarized by Richey (1922), and no detailed review will be presented here. In general, long, smooth, heavy ears with less than average number of kernel rows and shelling percentage produced greater average yields than did contrasting types.

III. Varietal Hybridization

Varietal hybridization has played a dual role in corn breeding. Varietal hybrids have provided foundation material from which many of the standard varieties were selected and stabilized by mass selection. In addition, it supplied some of the earliest information on yield heterosis in corn and thus indirectly lent encouragement to subsequent work on inbreeding and hybridization.

The religious ceremonies of many Indian tribes provided for the semicontrolled mixing of types characterized by different endosperm colors. The role of hybridization in the hands of the Indians may have played a much more important role in the development of corn varieties and types than is commonly recognized. Wellhausen *et al.* (1952) have suggested that varietal hybridization was one of the important factors in the present diversity of corn types found in Mexico. Varietal hybridization was sufficiently common in early colonial times to merit some attention. Beverley (1705) states:

There are four sorts of Indian corn, two of which are early ripe and two, late ripe; all growing in like manner The late ripe corn is diversified by the shape of the grain only—one looks as smooth and as full as the early ripe corn, and this they call Flint-corn; the other has a larger grain, and looks shrivell'd with a dent on the back of the grain, as if it had never come to perfection; and this they called She-corn. This is esteem'd by the planters, as the best for increase, and is universally chosen by them for planting; yet I can't see, but that this also produces the Flint corn accidentally among the others.

These observations suggest that the accidental or intentional intercrossing of these two types was not a new situation. Lorain (1825) some 100 years later describes the merits of mixing and intercrossing of the gourd seed ("She") and Flint types.

One hypothesis assumes that the dent types of corn had their origin from crosses between the Northern Flint and Gourd seed types. Anderson and Brown (1952) have suggested that this crossing was most intensive during the period from about 1800 to 1870. The report of Beverley indicated that it was well under way by 1700. It would appear logical to assume that it began immediately upon the introgression of

the gourd seed type into the area previously dominated by the flint types. This probably was some time after about 1000 A.D., since archeological evidence for the southeastern quarter of the United States reveals the presence of only the flint type corns.

Controlled experiments on varietal hybridization from which yield data were obtained were first reported by Beal (1877). Additional results were cited in the reports for 1880 and 1881-82. Detailed data were not presented, but he states that the hybrids tested outyielded the parents by amounts ranging from approximately 10 to 50 per cent. Beal's

TABLE II
COMPARATIVE PERFORMANCE OF VARIETAL HYBRIDS
INVOLVING DIVERSE ENDOSPERM TYPES

<i>Pistillate parent</i>	<i>Yield as a per cent of MINN. NO. 13</i>	
	<i>Pistillate parent</i>	<i>Cross</i>
Flour		
BLUE SOFT	96.7	132.5
Flints		
SMUTNOSE	110.8	127.6
KING PHILLIP	100.0	119.9
LONGFELLOW (NK)	100.5	119.6
LONGFELLOW (BURWELLS)	104.9	114.1
MERCER	91.8	97.3
Dents		
NORTHWESTERN	105.9	115.7
CHOWEN	99.0	114.9
RUSTLER	112.1	112.4
MINNESOTA NO. 23	96.7	110.9
SILVER KING	100.9	106.7
MURDOCK	80.3	101.6

interest in hybridization studies was derived in part from Darwin's studies (1877) on the same subject. Beal was interested in establishing co-operative experiments on corn hybridization. The report of Ingersoll (1882) was apparently a direct outgrowth of this co-operative attempt. Following the work of Beal and Ingersoll, an intensive investigation of varietal hybrids was begun at many different stations. No attempt will be made to review this early literature in detail.

The individual experiments involved in this early work must be interpreted with considerable caution. Many of the comparisons were based on single plots. Morrow and Gardner (1893) present some data on variation in yield among replicated plots of the same variety. In the

variety MURDOCK having a mean yield of 57.6 bu. the variation between the extremes of the four replicates was 11.9 bu. In the variety LEAMING, the observed range was 18.9 bu., with an average yield level of 70.1 bu. However, although the individual contrasts between parents and hybrids are poorly determined, the results from all experiments considered as a group follow a rather consistent pattern. Richey (1922) has summarized the data for 244 comparisons. Of this number, 82.4 per cent produced more, and 17.6 per cent produced less, than the average of the parents. Slightly over half of the crosses produced yields in excess of the higher yielding parent.

TABLE III
SUMMARY OF DENT X DENT HYBRIDS COMPARED
WITH THE HIGHER YIELDING PARENT

VARIETY X REID YELLOW DENT	<i>Gain</i>		<i>Loss</i>	
	<i>Bu. per acre</i>	<i>%</i>	<i>Bu. per acre</i>	<i>%</i>
CHAMPION WHITE PEARL	1.89	3.91	—	—
BOONE COUNTY WHITE	1.61	3.34	—	—
LEAMING (CHESTER'S)	1.58	3.67	—	—
CALICO	0.38	0.91	—	—
SILVERMINE	—	—	0.18	0.38
CRIMSON	—	—	0.42	0.98
REID YELLOW DENT	—	—	0.53	1.20
GOLDEN EAGLE	—	—	0.84	1.79
RILEY'S FAVORITE	—	—	1.73	4.13
LEAMING (MAXEY'S)	—	—	3.93	8.94

The results take on even more significance if they are summarized with respect to the characteristics of the parents. With very few exceptions flint-or-flour-dent crosses produced yields substantially greater than the higher yielding parent. In the dent X dent combinations the superiority of the hybrids was less consistent. In general the crosses exhibited the greatest superiority when the parents were high yielding and differed appreciably in type. Some idea of the difference in performance of variety hybrids is afforded by the data in Tables II (Hayes and Olsen, 1919) and III (Smith and Brunson, 1928).

The data in Table II represent averages for parents and crosses involving from one to four years of tests. All yields are expressed as a per cent of MINN. NO. 13, which was the staminate parent of all crosses. With but one exception, all crosses produced yields exceeding those of the higher yielding parent.

The data in Table III, representing averages covering a four- or five-year period, present a decided contrast. All of these hybrids involved REID as one parent and a locally adapted dent as the other parent. All comparisons are made with the higher yielding of the two parents. Only four of the crosses produced yields in excess of the higher yielding parent, and in each case the increase was small and nonsignificant.

Many of the early reports on varietal hybrids give instructions on how to produce hybrid seed. Some state that the method was being used by farmers. However, there is no information as to the extent of its use, and it seems probable that varietal hybrids were never planted on more than a small fraction of the corn acreage.

IV. Ear-to-Row Selection

The ear-to-row system of breeding was devised and put into operation at the Illinois Station in 1896 (Hopkins, 1899). Briefly the method involves the selection of a number of phenotypically desirable ears and the evaluation of these ears by means of a progeny test. The first attributes to receive attention were the oil and protein percentages of the grain. The results from the two series are rather similar, and we shall discuss only the results obtained with oil percentage.

One hundred and sixty-three ears of the variety BURR WHITE were analyzed individually for oil percentage of the shelled grain. A group of 40 ears having the highest oil percentage were chosen as foundation material for the "high" strain. A similar number of ears having a low oil percentage constituted the low strain. Each group was grown in an isolated plot with each of the parent ears planted as a separate entry. At harvest time ears were saved from the rows having the most desirable appearance. These were analyzed individually, and after the analyses were available 4 ears were saved from each of the 10 rows having the highest (or lowest) average oil percentage. This sample of 40 ears was then used to plant the ear-row plot the ensuing year. Various modifications of this general scheme were introduced at various times (Winter, 1929), but we shall not discuss these in detail. Woodworth, Leng, and Jugenheimer (1952) have presented a summary of the results after 50 years of such ear-row selection. Briefly the high strain has increased rather steadily from 4.70, which was the average value for the original 160 ears, to about 15 per cent. Similarly the low strain has decreased from 4.7 to 1.01. In the low strain, however, little progress was made after about 25 to 30 years. The reason for this appears to be that oil percentage is closely related to germ size. The low-oil strain has small germs and has also accumulated a number of mutations giving rise to

germless seeds. Apparently it is impossible to reduce germ size beyond a certain point and still retain seed viability.

Frequency distributions for the individual ears involved in the high and low series covering the first 10 years of the experiment were reported by Davenport and Reitz (1907). These are of considerable interest and are reproduced in Table IV. In the oil series after four generations of ear-row selection the original population had been separated into two entirely distinct populations. Separation continued at about the same rate until about 1925 (30 years), when functional variability in the low strain was largely exhausted. The high strain maintained about the same trend for the 50 years through which the experiment has been continued.

The contrast between this selection experiment and the one involving ear length mentioned in Section II is quite striking and deserves some comment. Ear-to-row selection differs from mass selection primarily in the progeny test. The compositing of ears under the mass selection scheme effectively obscures any information on progeny performance. The differences in the two selection experiments may be contrasted as follows:

Mass selection	Ear-to-row selection
No isolation	Isolation
No progeny test	Progeny test
Limited selection differential	Maximum selection differential

Certainly all of these differences are important, but it would be difficult to ascribe accurate weights to each of these causes. One other cause of the possible difference which is not related to the breeding systems is the relative extent to which each of these attributes is influenced by environment, oil percentage being the more stable of the two.

The long-continued effectiveness of selection in this experiment merits some speculation as to the genetic mechanism involved. At least two possibilities may be suggested. The results may be explained by a system of "internal" balance between chromosome regions and of "relational" balance between homologous chromosomes similar to that suggested by Mather (1942). It would appear that if such a situation exists it could readily account for the results obtained. However, some difficulty arises in accounting for the persistence of such a situation in the original random-breeding population. A second possible explanation would be the accumulation of successive mutations in the desired direction. This explanation also poses certain difficulties. Crosses between the high and low strains after some 40 generations of selection produced

TABLE IV
THE EFFECTIVENESS OF EAR-TO-ROW SELECTION FOR OIL PERCENTAGE^a

Seed	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	3.75	4.00	4.25	4.50	4.75	5.00	5.25	5.50	5.75	6.00	6.25	6.50	6.75	7.00	7.25	7.50	7.75	8.00	8.25	8.50	Average
1896										1	15	20	41	36	25	15	5	4	1											4.70
1897	H ^b 5.39								1			10	15	19	24	3	7	1												4.73
	L 4.03								5	7	9	7	7	5																4.06
1898	H 5.20										1	7	29	37	50	35	24	22	6	2	2	1								5.15
	L 3.65							8	9	31	31	19	9	1																3.99
1899	H 6.15											1		2	10	16	22	24	18	12	3									5.64
	L 3.47											23	8	1																3.82
1900	H 6.30													1	1	3	9	18	16	30	18	9	2	1						6.12
	L 3.33											6	3																	3.57
1901	H 6.77														2	3	10	13	26	21	28	15	7	1						6.09
	L 2.93																													3.43
1902	H 6.95														2	5	3	10	13	18	16	13	9	1						6.41
	L 3.00																													3.02
1903	H 6.73																1	10	10	19	18	21	13	5	2	1				6.50
	L 2.62																													2.97
1904	H 7.16																		3	9	8	12	15	18	18	8	6	2	1	6.97
	L 2.80																													2.89
1905	H 7.89																			4	9	19	15	21	17	19	7	5	4	7.29
	L 2.67																													2.58
1906	H 7.86																													7.37
	L 2.20																		1	5	9	24	16	32	20	8	2	3		2.66

^a From Table 1 Type and Variability in Corn, E. Davenport and H. L. Rietz, *Illinois Agr. Expt. Sta. Bulletin* 119, 1907.
^b H = high oil; L = low oil.

seed on F_1 plants which had the same oil percentage as the original variety BURR WHITE (Sprague and Brimhall, 1949). This would seem to require that any mutations favoring high oil percentage were almost exactly balanced by mutations in the low strain favoring a low oil percentage. Mutation appears to be such an erratic phenomenon that an exact balancing of opposing mutations appears somewhat unlikely.

After the favorable results from ear-to-row selection for chemical composition were known, the method was extended to various other attributes including yield. Extensive programs involving this breeding method were soon under way by both experiment stations and private concerns. The data are quite extensive, and we shall cite only two of the many possible illustrations.

Smith (1909) reports data on the effects of ear-to-row selection on several plant attributes, including plant and ear height. In this experiment approximately 24 ears were selected for the "high" eared group and a similar number for the "low" eared group. These were planted ear-to-row, the two plots being placed end to end. Among the progeny the first criterion of selection was productiveness and the second, height of ear. At the end of a six-year period the "high-ear" strain was approximately twice the height of the "low-ear" strain.

The selection practiced was effective in increasing the spread in plant and ear height between these two contrasting groups. It was also noticed that there was a close relationship between plant height and ear height. Furthermore height of plant or ear is closely associated with time of flowering, the shorter types being the earlier. In the 1907 and 1908 crop seasons it was noted that the low-ear strain was approximately one week earlier in flowering than the high-ear strain. Thus although no physical isolation of the two types was practiced, an effective physiological isolation was rapidly achieved owing to the association between ear height and time of flowering. The high- and low-ear strains were continued for some time, but no further reports on the effectiveness of selection were presented.

The results of ear-to-row selection for chemical and for various plant and ear attributes indicated that this breeding method was quite effective. It was natural, therefore, that it should be extended to an even more important characteristic, yield of grain. The early results from such studies indicated that the method was effective. However, as more data became available the results were often disappointing. The failure to obtain continuing favorable results was ascribed to various causes, and modifications of the ear-row method were devised to overcome the assumed limitations. Some of the modifications suggested and tried were detasseling of alternate halves of alternate rows, use of duplicate

plots for each ear row, the compositing of remnant seed from the high yielding rows, etc. None of these modifications appeared to increase the effectiveness of the method materially.

An experiment reported by Smith and Brunson (1925) provides more data on ear-to-row selection for yield than any other report available. Nine hundred and ninety ears were selected from a local variety and planted ear-to-row. At the same time a composite lot of seed representing these same ears was grown in an isolated plot to provide a standard for the measurement of progress. In addition this composite seed was used as a check on every tenth row in the ear-row evaluation plot. The check plots, presumably planted to identical seed, ranged in yield from 6.5 to 29.2 pounds per plot. The 40 highest and 40 lowest yielding ear rows, based on their performance in relation to adjacent checks, were chosen to form the high-yield and low-yield strains. In subsequent years 4 ears were saved from each of the 10 highest producing or lowest producing progenies to continue the strain. In each strain the most vigorous appearing plants were tagged prior to harvest, and the ears finally selected to represent either the high- or low-yield strain were chosen from these tagged plants. After a five-year period a "special" high-yield strain was established by means of a separate breeding plot. The foundation material was remnant seed of the 9 highest yielding ear-row selections from the high plot. Eight of these were used as females and detasseled and the highest yielding row used as a male. Eighty ears were selected from this mating plot for the next year's ear-row test plot. All the ear-row tests throughout the experiment were based on single rows. Since each of the three test plots were in separate areas, yields were not comparable. A comparison of the effectiveness of the selection practiced was made by comparing all strains in a separate yield test. Duplicate plots were used in the early years, and later four replications were used.

The results indicate that selection for low yield was quite effective. This was true even though the most vigorous plants were chosen in each of the low-yielding rows continued. Selection for high yield appears not to have been effective when compared with either the nonpedigree strain or the variety REID. Selection was also ineffective in the "special" high-yield strain. The failure of selection in these two strains may be caused in part by the inbreeding occurring in the breeding plots and also by the inadequacy of a single ear-row plot to provide an adequate measure of the genetic differences in yielding ability. From this and other studies it appears that the ear-to-row method of selection for yielding ability was discredited not because of genetic limitations of the method, but because of inadequate field plot technique. In every case,

ear-to-row selection was effective when the attribute involved was relatively little influenced by environment.

V. Selection within and among Inbred Lines

The first inbreeding experiments with corn were reported by Darwin (1877). However, these were continued for only a single generation and presumably had little effect on the future course of corn breeding. Inbreeding experiments were begun at the Illinois Station some time prior to 1900. The results of these studies were never reported in detail. Shamel (1905), who had worked in the Illinois program from 1898 to 1902, mentions the marked reduction in yield observed in material which had been self-fertilized for four generations. His suggestions for a practical method of corn breeding were such as to minimize inbreeding. His general conclusion was that:

It would seem that the improvement of our crops can be most rapidly effected with permanent beneficial results by following the practice of inbreeding, or crossing, to the degree in which these methods of fertilization are found to exist naturally in the kind of plant under consideration.

The first inbreeding experiments which led to an interpretation of inbreeding depression and the restoration of vigor upon crossing were reported by G. H. Shull. These studies were initiated because of his interest in the quantitative character, number of kernel rows per ear, rather than in corn breeding *per se*. In his first report (1908) Shull concluded:

1) that in an ordinary field of corn the individuals are very complex hybrids, 2) that the deterioration which takes place as a result of self fertilization is due to the gradual reduction of the strain to a homozygous condition, and 3) that the object of the corn breeder should not be to find the best pure line but to find and maintain the best hybrid combination.

In a later discussion of the pure-line method Shull (1909) states:

The process may be considered under two heads, 1) finding the best pure lines, and 2) the practical use of the pure lines in the production of seed-corn.

1) In finding the best pure lines it will be necessary to make as many self-fertilizations as practicable, and to continue these year after year until the homozygous state is nearly or quite attained. Then all possible crosses are to be made among these different pure strains and the F_1 plants coming from such crosses are to be grown in the form of an ear-to-row test, each row being the product of a different cross . . . 2) After having found the right pair of pure strains for the attainment of any desired result in the way of yield and quality, the method of producing seed corn for the general crop is a very simple though somewhat costly process.

Techniques for producing and testing lines have undergone considerable modification since this report in 1909, but the two procedures outlined still form the basis for most of the corn-breeding programs of today.

East (1908, 1909) presented data on the effects of inbreeding and cross breeding of maize. He was of the opinion that while the pure-line method of breeding was sound theoretically, it was not commercially feasible. As a more practical substitute he advocated, as also did Collins (1910) and many others, the use of varietal hybrids.

Inbreeding work on corn was begun at a number of stations following the early reports by Shull and East. The investigators appeared to be much more impressed by the reduction in vigor upon inbreeding than by the increased vigor following hybridization. This was not surprising in view of the relatively small number of lines available and the practice of maintaining any inbred line which could be propagated. Jones (1918) presented a summary of the results of the studies on inbreeding and cross breeding of corn conducted at the Connecticut Station. His suggestion that a new type of hybrid be produced from high-yielding single crosses eventually removed hybrid corn from the category of an intriguing theoretical possibility to that of a widely accepted commercial development.

1. Development of Lines

Maize is normally cross-pollinated and, therefore, artificial control is necessary to effect inbreeding. This is accomplished by covering the developing ear shoot, before silks have emerged, by a small glassine or parchment "shoot" bag. After emergence of the silks the appropriate tassels are bagged, and the following day the pollen within the bag is transferred to the silks (stigmas) of the desired plant. Many different methods have been developed for this pollen transfer (Sprague, 1942), and all are satisfactory in the hands of an experienced operator.

a. Standard Method. Self-fertilization is the most common form of inbreeding used. In this case pollen from a single plant is applied to silks of the same plant. Inbreeding is normally accompanied by selection. Plants to be inbred are selected for vigor, freedom from disease, etc. Since many desirable attributes are not apparent at the time of pollination, the plants are reselected at harvest time, any which have developed undesirable weaknesses of any sort being discarded. The selfed ears which survive this second selection are planted ear-to-row the following season. Selection is practiced both among and within progenies. Only the most desirable plants within the superior prog-

enies are used for further inbreeding. After 3 or 4 generations of self-fertilization the lines remaining will have become separated into distinct and relatively true breeding types. The major reduction in vigor occurs during the first few generations of self-fertilization. Jones (1939) has presented data indicating that reduction in plant height ceased after 5 generations and reductions in yield after 20 generations. In some instances sib lines separated after varying numbers of generations of self-fertilization were clearly different. These differences were assumed to be the result of spontaneous mutations rather than the expression of relict heterozygosity.

A number of other methods have been suggested for the isolation of lines. These may be divided into two general categories: (1) methods suitable for the direct isolation of lines from a heterozygous source; and (2) methods for the improvement of existing lines. We shall consider the direct isolation methods first.

b. Single-Hill Method. This modification of the standard method was suggested by Jones and Singleton (1934). It differs from the standard procedure in the replacement of the customary progeny row by a single three-plant hill in each generation of inbreeding. The space requirement for a single hill is less than for a progeny row; consequently, a larger number of progenies can be carried with a given land area. This method, therefore, minimizes the possibility of selection within progenies and increases the opportunity for selection among progenies. Since only one self-pollinated ear is saved from a hill at harvest time detailed pedigree records are not required.

Yermanos (1952) has presented some data on the relative-test cross performance of lines isolated by the standard and single-hill method, both sets of lines having a common origin. The results are not critical, since the inbreeding was done with approximately equal numbers of lines rather than a varying number of lines occupying an equal area in the nursery. The results obtained indicate a slight superiority in test-cross performance for the group of lines isolated by the single-hill method. However, the lines of single-hill origin exhibited a much greater degree of susceptibility to both root lodging and stalk breaking.

c. Pedigree Selection. Pedigree selection has been used most extensively in the Minnesota breeding program. The method consists in the selection of two inbred parents which in combination possess a series of desirable attributes and then isolating new lines from such crosses by the standard technique of self-fertilization and selection. Since the number of desirable lines of the appropriate maturity is usually limited, the common procedure has been to use one local and one exotic line in the foundation single crosses. The reports of Hayes and

Johnson (1939) and Johnson and Hayes (1940) indicate the value of this breeding approach.

A somewhat similar breeding scheme was used by Lindstrom (1939). This scheme was designated as cycling and involved the isolation of new lines from first-generation backcrossed material. Through successive repetition or cycles of this process it was hoped that progressive improvement of both the lines and their resulting hybrids could be achieved. Only limited data have been presented, but they suggest that the scheme may have some merit.

d. Homozygous Diploids. The production of homozygous individuals through the production of viable haploids has been suggested as a desirable breeding procedure by many workers. Two quite different procedures have been suggested for the quantity production of homozygous lines.

Burnham (1946) has suggested that it might be possible to build up an *Oenothera*-type multiple translocation involving each of the chromosome pairs. Such a stock could then be used as follows: (1) cross multiple translocation to heterozygous source; (2) examine pollen of F_1 plants and self-pollinate those exhibiting a high degree of sterility; (3) grow F_2 progeny and examine pollen for pollen abortion, saving only those having normal pollen; (4) outcross plants with normal pollen to a standard (i.e., carrying no translocations) stock; (5) grow test crosses and examine pollen, discarding all plants with partially sterile pollen. Test crosses exhibiting only normal pollen would be the desired type. The normal plant being tested would be the desired homozygote.

This method suffers from several obvious disadvantages. So far it has not been possible to build up the desired multiple translocation stock. Furthermore, corn does not exhibit directed segregation to any marked degree, and therefore a multiple stock would be difficult to produce and maintain. In addition the method does not provide for any great saving of time.

Einset (1943) cites unpublished data by Randolph in which a system of dominant genetic markers are used to detect haploids. Chase (1949, 1952a, 1952b) has used this scheme and reported on the frequency of haploids obtained from a number of different sources. Chase (1952a) reports that, as an average for the stocks studied, haploids occur with a frequency of about 1 per 1000, and among these haploids, selfed progeny were obtained in a frequency of about 1 in 10. Thus, as an average, 1 homozygous strain could be expected for each 10,000 seedlings tested. The frequency of 1 in 10,000 is of academic interest to the

corn breeder. The frequency which would be of importance would be the frequency of occurrence of commercially acceptable lines. No adequate data are yet available on this point.

The advantages claimed for this system of breeding are that it saves time and that the homozygous diploids obtained would represent a gametic sample having all of the advantages in superiority claimed for a gametic: zygotic sample (Stadler, 1944). In addition, plants would be subjected to severe selection during the haploid phase which would tend to eliminate all genotypes carrying deleterious genes. The effectiveness of such selection on combining ability was not established.

Thompson (1954) has presented data on test-cross performance of a number of homozygous diploids relative to the performance of lines derived by inbreeding, both groups of material being drawn from the same heterozygous source. Two unrelated sources were involved. In the first group 23 homozygous diploids obtained from GOLDEN CROSS BANTAM were compared with a random sample of 37 S_1 lines derived from the same source. All were crossed to a common tester and compared for a single year. Test-cross performance data revealed no significant difference between the two populations for either yield or variability.

The second group of homozygous diploids were derived from Stiff Stalk synthetic. These were compared with two other groups of lines from the same source. One group was made up of S_5 lines part of which had been derived from tested S_0 plants and part from previously untested lines. The S_5 lines as a group were considered to represent an essentially unselected sample. Five other lines, derived from the same source, had been subjected to repeated testing and were included to represent a selected sample. It should be pointed out that the lines of the highly selected group had been shown to be but little more than average in combining ability but were quite superior in resistance to lodging. All lines were crossed to a common tester. Most of the lines were tested for a two-year period. The results were in very good agreement with those from the sweet corn tests. There were no significant differences among the homozygous diploid and unselected S_5 population with respect to either yield or variability. In one year the mean of the selected sample was greater and in one year less than the means of either of the other groups. However, in neither case was the difference significant.

These results indicate that the theoretical advantages claimed for the homozygous diploid approach were not realized and that the homozygotes tested were not superior to a random sample of zygotes drawn from the same population. The usefulness of this approach for

corn breeding has not been established, but the method has many advantages for the study of certain theoretical problems.

e. Early Testing. The preceding breeding methods which have been discussed defer any test-cross evaluation of the line until a high degree of homozygosity is attained. In the early testing scheme inbreeding and test-cross evaluation proceed concurrently. The reasons for assuming that early testing might be advantageous have been presented by Lonquist (1950) and Sprague (1946, 1952) and will be reviewed here only briefly. Since the characteristics of an inbred line do not provide an adequate index as to the value of the line, and since this value must be determined by crossbred progeny tests, it appeared desirable to determine whether crossbred evaluation could be done at an earlier stage of the inbreeding process. Data from ear-to-row tests and from studies reported by Sprague (1939) indicated that individual selected ears from an open-pollinated variety exhibited marked differences in the yielding ability of their progeny. An identification of these high-yielding genotypes early in the course of inbreeding might permit the heavy discarding of inferior, and concentration of effort on the desirable, material at the stage of inbreeding when selection would be expected to be most effective.

The method of early testing was suggested by Jenkins (1935) and Sprague (1939), and the first critical data bearing on the method was presented by Sprague (1946). Data were reported on the test-cross performance of a series of S_0 plants and also on the test-cross performance of S_1 plants representing a seriated sampling of the original distribution. In both cases marked differences in combining ability were apparent. A series of lines derived by the early testing technique were contrasted with a selected group of lines then being extensively used in the production of commercial hybrids. The average performance, in single-cross combinations, of the lines derived by early testing was consistently superior to that of the line derived by the standard procedure.

Lonquist (1950) has reported additional data on the effectiveness of early testing. In this study a sample of S_1 lines of the variety KRUG were outcrossed to the parental variety and evaluated for yield. Fifteen lines were chosen for further study, with 8 representing the upper and 7 the lower portion of the yield range. Divergent selection for high and low combining ability, as measured by the test-cross performance, was practiced within each of the 15 lines from the S_2 through the S_4 generation. Selection for both high and low combining ability was quite effective in both groups throughout the period studied. However, the highest combining lines selected from the group representing the lower portion

of the S_1 yield range were no better than the poorest combining lines selected from the group representing the upper portion of the S_1 yield range.

The results presented by Sprague (1946) and Lonnquist (1950) indicate that early testing will aid in the detection of lines having high combining ability. Wellhausen (1952) has presented extensive data on the test-cross performance of S_1 lines and has shown that the early identification of superior combining ability may play a very important role in a breeding program.

Several workers have raised objections to the early testing procedure. For the most part these objections involve economic rather than genetic considerations. Where genetic considerations are involved, they are based on the presumed effectiveness of phenotype selection during inbreeding and therefore will be considered under Section V, 3.

The several schemes of recurrent selection were a logical outgrowth of the work on early testing. However, since these recurrent breeding schemes do not necessarily lead to the isolation of inbred lines, the discussion of these procedures is deferred to Section IX.

f. Convergent Improvement and Backcrossing. The methods of developing inbred lines considered thus far have had as their main objective the development of new lines. The other methods of inbreeding to be considered have as their objective the improvement of existing lines.

The concept of convergent improvement was developed by Richey (1927). Later Richey and Sprague (1931) presented data on a series of experiments designed to supply information on (1) types of gene action involved in yield heterosis and (2) the value of convergent improvement as a breeding method. The bearing of these results on heterosis will be discussed in Section X. Considered solely from a breeding standpoint convergent improvement involves the reciprocal addition to each of two inbred lines of the dominant favorable genes lacking in one parent and present in the other. Backcrossing to one line is continued for usually three or more generations. Selection is practiced during this procedure to retain as many as possible of the favorable dominant factors contributed by the nonrecurrent parent. Backcrossing and selection are performed in parallel, with each of the original lines serving as the recurrent parent in one series. Yields of lines compared after successive generations of backcrossing were consistently superior to expectation, indicating that selection had been effective in retaining a larger than average fraction of the dominant favorable genes. When these backcrossed lines were tested in single-cross combinations, the observed hybrid yields were also rather consistently superior to expectation.

These results indicated that by convergent improvement it was possible to obtain modified lines having improved performance and that this improved performance was transmitted to the hybrid progeny. Murphy (1942) has presented additional data which are in agreement with the above conclusions.

Convergent improvement and a somewhat simpler procedure, back-crossing, are both used in the improvement of established and tested lines. This procedure offers a convenient method for the introduction of some simply inherited characteristic into an established line. Yield, being a complexly inherited character, can be handled with somewhat less efficiency. The experience of many corn breeders has indicated that yield improvements can profitably be undertaken only with the very best of the inbred lines available.

g. Gamete Selection. This breeding scheme was proposed by Stadler (1944), and limited data bearing on the usefulness of the method have been presented by Pinnell, Rinke, and Hayes (1952). As proposed originally by Stadler, the method consists of crossing an elite line with a random sample of pollen from an open-pollinated variety. F_1 plants grown from such seed would differ only in the gametic complement contributed by the variety. The individual F_1 plants are to be self-fertilized and outcrossed to a tester. The elite line is also crossed to the same tester. Any test cross giving a performance superior to the elite $\times$ tester combination is presumed to have received a superior gamete from the open-pollinated variety. The theoretical advantage of the method lies in the argument that if zygotes of a given level of desirability occur with a percentage frequency of x , then gametes of equal desirability would be expected with a frequency of $\sqrt{x}$. Stadler also stressed the necessity for the continued sampling of open-pollinated varieties and suggested that gametic sampling offered a more efficient sampling procedure than the direct isolation of lines by standard inbreeding procedures. The method has one obvious disadvantage, namely, that the superior gametes identified cannot be isolated as homozygous zygotes. The final line resulting from the inbreeding of the superior F_1 plants can be considered as an improved rather than a new line, since it represents a mixture of the genes contributed by the superior gamete and the elite line. Richey (1947) has suggested that the corn breeder is interested not only in superior gametes, which in combination yield superlative zygotes, but in satisfactory zygotes as well; a satisfactory zygote being defined as one from which a superlative zygote may be isolated by further inbreeding and selection. From this he reasons that the $x: \sqrt{x}$ contrast is somewhat unrealistic and does not provide a real basis for the evaluation of this breeding scheme.

Hayes, Rinke, and Tsiang (1946) suggest that synthetics, single- and double-cross hybrids, etc., may be used equally as well as open-pollinated varieties in the gamete selection system. Pinnell, Rinke, and Hayes (1952) present data on gamete selection where the objective was to find a replacement in a specific double-cross combination. Three lines were used in the gamete sampling procedure—elite lines according to Stadler's terminology. These were crossed with either an open-pollinated variety or another inbred line. The results obtained indicated that desirable gametes could be obtained from either source, and new lines were isolated having superior performance. However, additional data are needed to provide a more thorough evaluation of this breeding system.

The use of the backcrossing, pedigree selection, or cycling schemes imposes one possible restriction which was not fully realized at the beginning of such studies. Unless special precautions are taken, the long-continued use of any of these breeding systems leads to an increasing degree of relationship among the surviving lines, with the likelihood of a deleterious influence upon the resulting hybrids among them. This difficulty has been partially met by assigning the existing lines to one of two separate groups A and B. The component lines of a hybrid, which is to be used as foundation material for the isolation of new lines, are chosen so that the two parental inbreds are members of the same group. Thus continued repetition of any of the above breeding systems will lead to increasing relationship within a group but maintain the diversity between groups. The final double cross to be made and tested would be of the type $(A \times A) (B \times B)$.

From a consideration of the inbreeding schemes discussed above it is apparent that there exists a diversity of opinion as to the function and desirability of inbreeding. One viewpoint assumed that absolute homozygosity is the desired goal, and the more rapidly this can be achieved the better. The other extreme assumes that inbreeding is a necessity for propagation and provides a convenient mechanism for the isolation of genotypes which may then be subjected to a critical evaluation. The harmonization of these extreme viewpoints must be based on the accumulation of additional data.

2. Correlation between Characters of Inbreds and Hybrids

As mentioned previously selection for plant and ear characters is practiced during the course of inbreeding. Studies have been reported by a number of investigators on the relation between various attributes of an inbred line and the same attribute or yield of its hybrid progeny. Kiesselbach (1922) reported a general relation between the yielding

ability of an inbred line and that of its hybrid progeny. Richey (1924) and Richey and Mayer (1925) found that certain inbred lines were quite prepotent in transmitting high yielding ability to their progeny. Hayes (1926) presented evidence that yield was significantly correlated with other characters which were expressions of vigor. Nilsson-Leissner (1927) and Jorgenson and Brewbaker (1927) reported correlation between various attributes of inbreds and hybrids which were judged of sufficient magnitude to be useful in selection. The most detailed and comprehensive correlation studies were those reported by Jenkins (1929). These studies involved correlations among characters in inbred lines, in F_1 single crosses and between characters of the inbred line and various characters of their crossbred progeny. The correlations involving yield as one variable are of greatest interest. Within inbred lines positive and significant correlations were obtained between yield and plant height, ear length, ear diameter, shelling percentage, and number of ears per plant. Significant negative correlations were obtained for yield and chlorophyll grade, date of silking and shrinkage of the harvested ears. Within the parent-progeny series and also within the F_1 hybrids significant and positive correlations were obtained between yield and date of silking and tasseling, plant height, ear length and diameter, number of ears per plant, and number of nodes per plant. Only a few of the correlations were of sufficient magnitude to have definite predictive value. The highest multiple correlation involving yield was $+0.42$. This correlation involved yield of the crossbred progeny and characters of the inbred indicative of vigor, namely, plant height, number of nodes, number of nodes below the ear, and yield.

Hayes and Johnson (1939) reported correlations between the yield of inbred-variety crosses and various attributes of the inbred parents. Yield was positively and significantly correlated with each of the 12 attributes studied. The multiple correlation between yield and the 12 attributes of the inbred parents was 0.666. Where direct comparisons are possible this is a somewhat closer relationship than found by Jenkins. The type of test crosses used may partially account for this difference. In Jenkins's study the test crosses were F_1 hybrids. Under such conditions any departures from additivity would be common to all plants of a given mating and would tend to reduce the magnitude of the observed correlation. In the inbred-variety crosses, each plant within a plot might have a different genotype. Under such conditions nonadditive deviations would at least partially cancel.

All of these correlation studies were conducted prior to the concept developed by Panse (1940) that phenotypic correlations are made up of two portions, one arising from environmental and the other from

genetic effects. Had this technique been used in the above studies, it appears that estimates of the genetic correlations might have been somewhat different than the phenotypic correlations reported.

Robinson, Comstock, and Harvey (1951) have presented both phenotypic and genetic correlations involving a series of eight attributes in crosses among F_2 plants derived from three single crosses. In a few cases the two estimates of association differed appreciably. Ears per plant was the only attribute found to have high positive genetic correlation with yield. These authors illustrate how genetic correlations may be used in the construction and evaluation of selection indices.

However, even though the individual correlations reported are, in general, so low as to have limited predictive value, selection during inbreeding still serves a very important function. The earlier concept that any inbred line which could be maintained was a potentially valuable line has been discarded. The present concept is that inbred lines must measure up to certain standards of vigor and productiveness as a line before they merit testing. An inbred which can be maintained with difficulty is essentially worthless from the standpoint of commercial seed production, even though it may produce very high-yielding outcross progeny. Such a line might be useful as source material for improvement but would not be useful commercially as long as serious propagation difficulties were encountered.

3. Effect of Selection on Yield of Hybrids

Selection during inbreeding may conceivably serve more than one purpose. First, as mentioned above, it eliminates lines which would have limited or no commercial value. Second, it may insure that propagation is confined to the most vigorous plants, thereby materially raising the general standard of excellence of the ultimate lines without respect to their crossbred performance. Third, the selection practiced during inbreeding may be beneficial in improving the performance level of the final hybrids. Obviously information on the first possibility would be difficult to obtain. We shall be concerned primarily with only the third possibility stated.

Richey and Mayer (1925) presented data indicating that no general advantage in crossbred performance was derived following three generations of selfing. The differences between the hybrids made after the second and third generations of selfing were somewhat erratic but as an average favored the more highly inbred parents. Davis (1934) reported that high-combining S_2 lines, as measured by inbred-variety cross, also exhibited high combining ability when tested as S_4 and S_5 lines.

Jenkins (1935) compared a series of inbreds derived from the varieties LANCASTER and IODENT from the first through the eighth generation of inbreeding, excepting the seventh. These were tested as inbred-variety crosses, KRUG being used as a common tester. He concludes:

Selection was ineffective in isolating strains whose crosses differed from those of their parents in productiveness or in any other characters studied. The inbred lines acquired their individuality as parents of top-crosses very early in the inbreeding process and remained relatively stable thereafter.

This interpretation has been questioned by Richey (1945). By a system of combining various generations he concluded that selection had been effective in Jenkins's material as measured by the performance of $S_2 - S_3$ vs. $S_6 - S_8$ hybrids. Singleton and Nelson (1945) have presented data which they interpreted as indicating an improvement in combining ability during the course of inbreeding. Interpretation of statistical significance in this case depends upon the specific question the data are requested to answer. If conclusions are to be confined to the particular set of lines used in this experiment, the effect of generations of inbreeding is correctly judged significant. However, if one considers this group to represent a random sample of lines about which inferences are to be drawn, the appropriate test indicates generations of inbreeding to be nonsignificant. This does not imply that a trend was absent. It indicates that any trend which may exist is small in comparison with the observed differences among lines over the generations of inbreeding studied.

Sprague and Miller (1952) have presented additional information bearing on the general problem of the effectiveness of selection in modifying hybrid performance. Two separate groups of six lines each were involved. Using remnant seed, all possible F_1 combinations were made in each group, within each of the five generations of inbreeding represented. The mean square associated with "generations" was broken down into a "linear" and a "residual" component. Had selection been sufficiently effective to modify hybrid performance materially, a linear trend over the successive generations of inbreeding should have been evident. No statistically significant trend was observed in either experiment. A linear trend would have as its basis a change in general combining ability. Changes in specific combining ability during the course of inbreeding were quite apparent. The general results from these two experiments, therefore, appear to be in agreement with the data presented by Jenkins (1935) and with his interpretation.

Payne and Hayes (1949) have presented data contrasting the test-cross performance of a series of F_2 plants and their F_3 progenies. They conclude that the testing of the F_2 's was of doubtful practical value.

However, their results indicate quite clearly that the F_2 's with the highest combining value produced a proportionally larger percentage of high-combining F_3 progenies than the F_2 's with low combining values.

The controversy over the effectiveness of selection during inbreeding is still unsettled. It should be remembered, however, that this difference of opinion concerns only the question of the effectiveness of phenotypic selection in modifying hybrid performance. The effectiveness of selection in modifying the characteristics of the lines themselves is generally accepted.

VI. Evaluation of Inbred Lines

The development of inbred lines poses no problem equal in complexity to those involved in the evaluation of lines. The final evaluation of even the most carefully selected inbred line must rest upon its performance in hybrid combinations. For a time it was customary to produce and test as many as possible of the F_1 crosses among or between groups of lines. Inbreds were retained or discarded on the basis of their mean performance. This system of testing became entirely inadequate as ever increasing numbers of lines became available for testing. A search was made for a simpler and less costly testing procedure.

Jones (1922) presented data on inbred-variety crosses, but his interest was in relative performance rather than as a method of evaluating lines. Lindstrom (1931) also presented data on inbred-variety crosses. He emphasized that certain lines were very prepotent for ear type, disease resistance, and uniformity of maturity and suggested the commercial use of such hybrids. Davis (1927) presented data on inbred-variety crosses, using this procedure to estimate the combining ability of S_2 lines. A more detailed report of the same experiments was made in 1934. The most extensive report on the performance of inbred-variety crosses was presented by Jenkins and Brunson (1932). Correlations were calculated between the mean performance of lines involved in a series of single crosses and the performance of these same lines in inbred-variety crosses. Correlations between yields for the two types of crosses ranged from 0.53 to 0.90 for the different groups involved. The pooled correlation for two groups, involving 77 lines, was 0.75. On the basis of these studies they concluded that it would be safe to discard the lower yielding 50 per cent of the lines under test without any serious risk of losing valuable material. The remaining 50 per cent would be tested further in single-cross combinations.

Johnson and Hayes (1936) presented data on the inbred-variety

cross performance for a number of lines derived from the variety GOLDEN BANTAM. Eleven of these lines were also tested in all possible combinations as single crosses. The lines exhibiting low combining ability, as measured by inbred-variety crosses, were as a rule below average in their mean single-cross performance. Conversely the highest yielding single-cross combinations involved lines exhibiting above average performance in inbred-variety crosses. On the basis of these data they concluded that inbred-variety crosses provided a rapid and satisfactory method for the preliminary evaluation of inbred lines.

1. Genetic Diversity and Inheritance of Combining Ability

It has been common experience that the better double crosses involve inbred lines derived from two or more varieties. The importance of this diversity of origin has been stressed by several investigators. The general approach to studies on this problem has been to isolate new inbred lines from a series of desirable single crosses. After the lines were inbred for three or four generations they were evaluated in inbred-variety crosses. The superior lines were then evaluated in single-cross trials and the single-cross performance contrasted on the basis of the relationships involved in the parental single crosses, i.e., unrelated, one or both parents common.

Wu (1939) has shown that lines of related origin consistently produce lower yielding single crosses than lines having only one or no parents in common. Hayes and Johnson (1939) report data on the same problem. In crosses between lines, unrelated in origin, 28 of 43 single crosses were equal or superior to the standard double crosses in yielding ability. In the groups having one or two parents in common only 6 of 15 and 1 of 6 crosses, respectively, were equal or superior to the standard double-cross checks. Johnson and Hayes (1940) presented additional data indicating that there was a statistically significant difference in single-cross performance of related and unrelated lines. Eckhardt and Bryan (1940a) and Cowan (1943) have also stressed the importance of genetic diversity in the production of high-yielding hybrids.

Studies on the inheritance of combining ability have been reported by Johnson and Hayes (1940), Cowan (1943), and Green (1948a, 1948b). In each of these studies single crosses used as foundation material were classified as high $\times$ high, high $\times$ low, and low $\times$ low on the basis of previous tests of the component lines. New lines isolated from the low $\times$ low single crosses were significantly lower in yield when tested in single-cross combinations than lines isolated from either the high $\times$ low or high $\times$ high single crosses. The study reported by Green

(1948a, 1948b) differed somewhat in design in that the new lines were tested against two testers. When u.s. 35, a double cross, was used as the tester the frequency distribution of lines derived from high $\times$ low and high $\times$ high parentage were not significantly different.

However, when the open-pollinated variety, Black's yellow dent, was used as the tester parent the differences between the high $\times$ high and high $\times$ low frequency distributions were highly significant. These studies indicate that the detected segregation for combining ability as measured is a function of the genetic characteristics of the tester parent as well as of the inbred lines. Such a situation may result from a masking effect of certain gene frequencies or may arise from certain types of nonadditive gene effects.

2. *Line $\times$ Tester Interaction*

The proper choice of testers is a very important problem in corn breeding, but one which has received relatively little attention. Some of the earlier work which has a bearing on this problem (Section VI above) was concerned only with the relationship between inbred-variety crosses and average performance in a series of F_1 single crosses. The relationship was found to be sufficiently close to have considerable predictive value, but such studies provided no direct measure of the magnitude of the line $\times$ tester interaction.

Studies directed at various aspects of the line $\times$ tester problem have been reported by Federer and Sprague (1947), Matzinger (1953), and Keller (1949). Federer and Sprague (1947) analyzed a series of 11 top-cross experiments involving two or more testers. The number of lines per test ranged from 6 to 98. It was assumed that the lines, testers, and replicates were random samples of the lines, testers, and replicates which might be used.

Estimates of the variance components for lines, testers, and errors were obtained. Unbiased estimates of the ratio of variance components were obtained for σ_L^2/σ_E^2 and σ_{LT}^2/σ_E^2 . As an average for the 11 experiments these were found to be 0.58 and 0.23, respectively. Yates (1940) proposed a formula for estimating the average gain in combining ability due to the selection of the apparently best instead of a random line. This formula was modified to include the effect of testers:

$$\frac{\sigma_L^2}{\sqrt{\sigma_L^2 + \frac{\sigma_E^2}{rt} + \frac{\sigma_{LT}^2}{t}}} \bar{x}_L$$

where $\bar{x}_L$ is the average extreme deviate in positive standard deviation units for population of size L . The substitution of the observed esti-

mates in this formula indicated that for a fixed number of plots the greatest gain in total combining ability could be expected from an increase in number of testers, followed in order by an increase in number of lines and, least important, by an increase in number of replications.

The results reported by Matzinger (1953) attack the same general problem from a somewhat different standpoint. On the assumption that an increase in number of testers is desirable, can such testers be used most efficiently as inbreds, single crosses, or double crosses? Sixteen inbred lines were involved in the study. This group was considered as a random sample of lines having sufficient proved merit to be useful in commercial seed production. The lines were arbitrarily divided into two equal groups, one group considered as lines to be tested and the second group as testers. The eight lines of the tester group were used as lines, as single crosses, and as double crosses. The eight lines tested were placed in essentially the same rank when averages were obtained over all testers within a given type. However, the variance component estimates of the interactions of inbred testers $\times$ lines, single-cross testers $\times$ lines, and double-cross testers $\times$ lines for yield in bushels per acre were 17.22, 11.90, and 6.46, respectively. These results indicate that as the genetic variation within a tester parent increased, the line $\times$ tester interaction decreased. With any one tester of limited genetic variability the observed performance was highly specific and would have limited predictive value for estimating performance with a second unrelated tester.

Hull (1947) has suggested that the better inbred lines now in commercial use are worthless as testers for general combining ability because of a tendency to obscure differences among the lines under test. Keller (1949) has examined this possibility by means of yield data from 22 yield trials involving all possible combinations among a group of inbred lines. These 22 experiments were selected because of variation in average combining ability for the lines represented. Each experiment was divided into two groups, one involving the high-combining lines and the other the low-combining lines. Variance component estimates were obtained for s_L^2 and s_{LT}^2 for each group within each experiment. The individual estimates were poorly determined, but as an average over the 22 experiments the variance component for s_{LT}^2 was somewhat greater for the high-combining testers. Thus any masking effect must have been of limited importance.

3. General and Specific Combining Ability

The preceding presentation has served to emphasize that some of the problems arising in the evaluation of lines are a part of the more

general problem of the types and relative importance of gene action involved in heterosis. Different types of testers may give quite different weights to the types of gene action being estimated. Sprague and Tatum (1942) have divided the gene action concerned with combining ability into two categories, general and specific. General combining ability is measured as though it were due predominantly to additive gene action. Specific combining ability then includes all effects which cannot be accounted for on the additive scheme. These may be the result of dominance, epistasis, genotypic-environmental interactions, etc.

Estimates of the variance of general (σ_G^2) and specific (σ_S^2) combining ability were obtained from a series of single-cross yield trials. In general it was found that with previously tested material the variance for specific combining ability was somewhat greater than the corresponding variance for general combining ability. In the few experiments available this situation was reversed when relatively untested lines were used. This was attributed to the selection for general combining ability which had been practiced in previous tests. In the original population of unselected lines marked differences in top-cross performance would be expected, and the lines having poor combining ability would be discarded. Subsequent testing would result in the elimination of additional lines. Any sample of lines which has survived repeated testing would possess only a fraction of the variation in general combining ability originally present, and thus estimates of the variance of general combining ability would be reduced.

Estimates of the relative magnitude of σ_G^2 and σ_S^2 from individual experiments may be of limited value. The point of major interest is the constancy of such estimates when the experiments are repeated over a series of locations or years. Rojas (1951) has developed mathematical models for estimating the variances of general and specific combining ability from groups of single-cross experiments. This model was applied to a series of single crosses which had been tested at two or more locations for a three-year period (Rojas and Sprague, 1952). When estimates of the σ_G^2 and σ_S^2 were obtained from the individual experiments, the results were in general agreement with the results obtained by Sprague and Tatum (1942). However, when σ_G^2 and σ_S^2 were estimated over all years and all locations they were of essentially equal magnitude. The interactions of general and specific combining ability with locations and years were of particular interest. The interactions involving general combining ability (σ_{GL}^2 and σ_{GY}^2) were considerably smaller than the corresponding interactions involving specific combining ability. These results were interpreted to mean that the geno-

type-environment interaction was an important constituent of the variance of specific combining ability.

The experiments used in the above study involved previously tested lines. As mentioned earlier, this previous selection might operate to reduce the magnitude of σ_G^2 and the various interactions involving general combining ability. Consequently studies are being repeated using untested S_1 lines. The lack of previous testing and the use of S_1 material both should operate to increase the estimate of σ_G^2 and the interactions involving general combining ability with locations and years relative to the corresponding estimates for specific combining ability. Only a single year's data are now available. For this single year estimate of σ_G^2 and σ_s^2 were rather similar. The estimate of σ_{SL}^2 was approximately three times that of σ_{GL}^2 . The results, therefore, are in essential agreement with the results presented by Rojas and Sprague (1952) and support the original suggestion that estimates of the variance of specific combining ability are made up, in large part, of the genotype-environment interactions.

4. *Hybrid $\times$ Location and Hybrid $\times$ Year Interactions*

If the relative performance of hybrids were little influenced by environment, then tests conducted at a single location for a single year would suffice to provide adequate information for elimination or recommendation. However, this desirable situation does not obtain, and it is necessary to conduct repeated trials. Knowledge of relative magnitude of hybrid $\times$ location or hybrid $\times$ year interaction would provide some information as to the extent of testing required for accurate evaluation of relative performance. Such information is very largely lacking.

Sprague and Federer (1951) have presented data on a series of top-cross, single- or double-cross yield trials conducted at two or more locations or for two or more years. The mathematical model assumed was rather similar to the one mentioned in Section VI, 2. Unbiased estimates were obtained for the ratios s_{HD}^2/s_E^2 , s_H^2/s_E^2 , and s_{HY}^2/s_E^2 as well as estimates for the s_D^2 (districts) s_H^2 (hybrids) and s_Y^2 (year) effects. In the series involving location effects 10 top-cross, 18 single-cross, and 25 double-cross experiments were available. In the top-cross tests the averages of the ratios s_{HD}^2/s_E^2 and s_H^2/s_E^2 were of essentially equal magnitude. In the single- and double-cross tests s_{HD}^2/s_E^2 was roughly half the value for s_H^2/s_E^2 . Twenty-three single and thirty-two double-cross experiments were involved in the series estimating year effects. In the single-cross series s_{HY}^2/s_E^2 was approximately 50 per cent greater than

$\frac{2}{s_H^2}$, whereas for the double-cross experiments the two ratios were roughly of the same magnitude, $\frac{s_H^2}{s_E^2}$ being somewhat the larger.

The experiments designated as top-cross represent a heterogeneous group with respect to the tester parent used, ranging from single crosses to open-pollinated varieties. Considering only the single- and double-cross experiments the results suggest that the hybrid $\times$ location or year interaction is quite important and that single crosses must be tested at more locations or for more years or both, than double crosses, to obtain the same degree of precision. In other words as the heterogeneity of the material under test increases, the estimated interaction with environment decreases. The various estimates obtained from these studies together with cost data were used to calculate the optimum number of years, locations, and replicates for a fixed cost and also the costs per plot per unit average genetic advance with varying numbers of plots per location and varying numbers of locations.

The material reviewed in this and preceding sections provides some basis for generalization with respect to testing procedures. The choice of a suitable tester depends in large part upon the use to be made of the lines. If one is seeking a replacement for a specific line in a double-cross combination, then the most efficient tester would be the opposing single cross. The two inbred parents of this single cross might also be used, but this procedure would be both more time consuming and more expensive.

A more general situation might be one in which a group of new lines would be available for testing but without any predetermined plan for their use in a specific hybrid combination. Under these conditions the first evaluation might well involve a heterozygous and heterogeneous tester and thus provide a measure of general combining ability or additive gene action. The lines remaining would be tested further in either single or three-way crosses to obtain information on performance in specific combinations.

Where specific combining ability is of primary interest, tests must be conducted at more locations or over a longer period of years to provide reliable information than is true where general combining ability is of first importance.

VII. The Prediction of Double-Cross Performance

The number of combinations and permutations of items taken four at a time increases very rapidly with an increase in the total number of items. For this reason it is quite impractical to produce and evaluate all possible double-cross combinations among even a small number of lines. Ten inbred lines can be combined to produce 45 single- and 630

double-cross combinations, disregarding reciprocals. Obviously some method of evaluation other than actual testing would be desirable.

The first studies on this problem were reported by Jenkins (1934). Eleven lines were used and data were obtained on (1) inbred-variety crosses of these lines, (2) 53 of the possible single-cross combinations, and (3) 42 of the possible double-cross combinations. These data were then used to contrast the relative effectiveness of four different methods of prediction. These were: (*a*) the mean performance of the 6 possible single crosses among any set of 4 lines, (*b*) the average performance of the four nonparental single crosses, (*c*) the average performance of a set of 4 lines over a series of single crosses, and (*d*) the average top-cross performance of a group of 4 lines. The agreement between predicted and observed performance of the 42 double crosses was measured by means of correlations. There was little difference between methods *a*, *b*, and *c*, with method *d* providing the poorest estimate of the four tried. These four methods of prediction involve somewhat different assumptions with respect to the type of gene action involved. Methods *a*, *c*, and *d* all assume additive gene action, i.e., a gene contributed by any line will produce its characteristic effect regardless of the order of pairing. The accuracy of the estimation of these additive effects differs somewhat for the three methods. Method (*b*) permits the recognition of nonadditive effects arising from dominance, epistasis, etc. In general the correlations between prediction and observation were somewhat higher with method (*b*) than with any of the other methods tried.

The effectiveness of method *b* has been checked by several workers. Doxtator and Johnson (1936) presented data on the observed and predicted yields for 7 double and 2 three-way crosses. Anderson (1938) presented additional data on 15 double crosses and found a good agreement, $r = 0.90$, between prediction and observation. Hayes, Murphy, and Rinke (1943) presented correlations between prediction and observation on yield and moisture percentage for a group of 114 double crosses. The correlations were 0.48 for yield and 0.21 for moisture content. These values are somewhat lower than those reported by other workers. The single-cross yields used for prediction and the actual double-cross yields were obtained in different years. The genotype-environment interaction would operate to reduce the estimated correlation.

The use of single- and three-way-cross performance data for the prediction of double-cross performance has become a standard breeding procedure. Schemes have been devised for the use of punched card equipment to facilitate the routine prediction computations (Millang and Sprague, 1940; Combs and Zuber, 1949).

1. Order of Pairings

Variation in double-cross performance attributable to the order of pairing of the component lines may be ascribed either to dominance or to some other type of nonadditive gene effects. Doxtator and Johnson (1936) reported that order of pairing had a pronounced effect on both the predicted and observed double-cross yields. This problem has been studied in some detail by Eckhardt and Bryan (1940a, 1940b). Representing lines from one varietal source as A and B and lines from a different source as Y and Z , comparisons were made between crosses of the type $(A \times B)(Y \times Z)$ and $(A \times Y)(B \times Z)$. The double crosses producing the highest yields were of the $(A \times B)(Y \times Z)$ parentage. The variance associated with "method of pairing" was found to be highly significant for acre yield. Measurements were made of several plant and ear attributes within each type of cross. Variances for ear height and ear length were significantly lower in the $(A \times B)(Y \times Z)$ crosses. Variances for plant height and ear weight were also lower in the same type of cross but not significantly so. Similar studies were made using six early (E) and eight late (L) lines. Variances for silking date, ear height, ear weight, length, and diameter were significantly less for the $(E \times E)(L \times L)$ combinations.

Pinnell (1943) presented data on yield and variability for the three double-cross permutations possible with four inbred lines. Of the four lines used, two were characterized by tallness, lateness, big ears, large leaf area, and large number of kernel rows per ear. The other two lines exhibited the opposite characteristics. Individual plant data were recorded for date of silking, plant height, ear leaf area, percentage of ear moisture, ear length, and kernel row number within each of the six single- and three double-cross combinations. One of the $(E \times L)$ combinations exhibited the least variability and the other similar combination, the greatest variability. There were no significant differences among the means of the three hybrids for any of the attributes studied. In this particular study, therefore, neither deviations from additivity nor segregation effects were important. In the studies reported by Eckhardt and Bryan (1940a, 1940b) one or both of these possible factors were involved and shown to influence both the mean and variability. In the study reported by Pinnell, members of each set of two lines were chosen for phenotypic similarity. The phenotypic similarity did not involve sufficient genotypic similarity for segregation to be an important factor in variability. In the other study lines A and B , etc., were derived from the same varietal source and therefore may be presumed to have a considerable number of genes in common. This would

provide greater opportunities for the expression of both segregation and nonadditive gene effects.

VIII. Multiple Hybrids and Synthetics

Multiple hybrids and synthetics have one element in common: both terms through common usage are usually restricted to combinations involving more than four inbred lines.

Studies on the performance of multiple crosses have been rather limited. The principal theoretical advantage suggested for the method is the somewhat greater variability expected in the commercial crop. Where an increased variability is desired it can be achieved more easily and economically by the blending of two or more double crosses possessing the desired differences in maturity. Data on the performance of multiple hybrids have been presented by Kiesselbach (1933) and Sprague and Jenkins (1943). In the studies reported by Kiesselbach the primary objective was the contrast between first- and second-generation seed. The results presented cover a varying period of years, and a direct comparison between double and multiple crosses is not possible. Sprague and Jenkins (1943) present data on the relative performance of 4 double and 8 multiple (16 line) crosses for a three-year period. The average yield of the multiple crosses was somewhat lower than the average of the double crosses. However the highest yielding multiple cross was only slightly lower yielding than the best double cross tested. The difficulty in isolating and identifying a large number of lines, all of which have high combining ability *inter se*, seriously limits the commercial usefulness of multiple crosses.

A number of studies have been reported contrasting the use of F_1 and F_2 single-cross seed for the production of double crosses. Kiesselbach (1930) has reported that double crosses between F_2 -generation plants exhibited as satisfactory performance as their counterparts produced between F_1 -generation plants. This would be expected. The variation among gametes produced by F_2 plants would be somewhat greater than the corresponding variation among gametes from F_1 plants, but in the absence of selection there would be little opportunity for a marked change in gene frequency. However, under some conditions changes in gene frequency may be important. Hayes, Johnson, and Doxtator (1931) reported that double crosses produced from F_1 , F_2 , and F_3 single-cross plants produced relative yields of 100, 103, and 112, respectively. The explanation for these results must be sought in some change in gene frequency.

F_2 or advanced-generation plants of single crosses are not used for the commercial production of double crosses except in emergencies. The

use of plants of these advanced generations results in lower yields in the seed field and in poorer grading characteristic of the harvested seed crop. The use of F_2 seed, either single- or double-cross, for commercial planting is also a costly procedure. The formula presented by Wright (1922) indicates that the expected reduction in yield would be 50 and 25 per cent for the F_2 generations of single and double crosses, respectively. The data presented by Neal (1935) approximate these expected reductions very closely. Data presented by Richey, Stringfield, and Sprague (1934) for a series of double crosses and by Kiesselbach (1933) for single-, double-, and multiple-cross combinations indicate that substantial yield reductions occur in every instance.

The term "synthetic variety" is used to designate the advanced generations of a multiple hybrid increased by open pollination. Some reduction in yield is to be expected under such conditions. Studies on the agreement between the observed and calculated yield reductions have been concerned entirely with single, three-way, and double crosses. Such results have served as a basis for extrapolation to account for the observed and theoretical performance of synthetics in general.

Neal (1935) reported yields for the inbred parents, F_1 and F_2 generations of 10 single, 4 three-way, and 10 double crosses. The agreement between observed and predicted F_2 yields was good for each type of cross. Predicted yields were calculated using the formula presented by Wright (1922):

$$F_2 = F_1 - \frac{(F_1 - P)}{N}$$

This formula is based on the assumption of arithmetic gene action and the close agreement between observation and prediction in the data presented by Neal (1935) and Kinman and Sprague (1945) has been interpreted as indicating the unimportance of nonadditive gene action. The adequacy of the arithmetic assumption for hybrids of greater complexity than single crosses is due in part to the manner in which the formula is used. This may be illustrated by unpublished data obtained in the corn-breeding program at Ames, Iowa. Seed was prepared of two series of double crosses. In one series the three possible permutations among a set of 4 lines gave quite similar predicted yields. The other series included lines for which the three permutations gave quite dissimilar predicted yields. Three different groups of 4 lines each were involved in the first series and 6 groups of 4 lines each in the second series. Yields of the F_1 and F_2 generations were obtained for each of the 27 double-cross combinations. F_1 yields also were obtained for all of the possible single crosses. The pertinent part of the analysis of variance

for the two experiments involving F_1 and F_2 double crosses is given below:

	<i>D.F.</i>	<i>Mean Square</i>	
		<i>D.C. F_1</i>	<i>D.C. F_2</i>
Within sets	18	32.29	3.85
Remainder	53	3.63	3.37

The variation among permutations within a set of 4 lines was highly significant. This was expected, since 6 of the 9 sets of 4 lines were chosen because of these predicted differences. In the F_2 series the variation among permutations within a set was not significant. This indicates that any significant departures from additivity apparent in the original double cross become of limited significance in the F_2 generations of these same double crosses. If one is interested primarily in expected F_2 performance, the formula may well be written

$$F_2 = \bar{F}_1 - \frac{(\bar{F}_1 - \bar{P})}{N}$$

where the $\bar{}$ denotes the average. Thus $\bar{F}_1$ in the case of a double cross would be the average of the 6 possible singles among a set of 4 lines rather than the 2 parental singles. This averaging, in itself, tends to eliminate the effects of nonadditive gene action. In the studies reported by Neal (1935) and Kinman and Sprague (1945) this interpretation of the prediction formula has been used.

It is readily apparent from the formula given above that the yield of the advanced generation of a multiple cross (synthetic) is dependent upon four factors: (1) the number of lines (N) involved, (2) their mean performance (P) as lines, (3) the mean performance of all possible combinations among the N lines. The fourth factor, which can be largely disregarded in corn, is the amount of self-fertilization. Hayes and Garber (1919) were the first to suggest the possibility of the commercial utilization of synthetics. Hayes (1926), Kiesselbach (1933), and Sprague and Jenkins (1943) have presented data indicating that synthetics were rather similar to open-pollinated varieties in performance. The lines used in these studies, however, did not represent a selected group with respect to combining ability.

Kinman and Sprague (1945) reported yields of grain for 10 inbred lines, the 45 possible single-cross combinations, and the F_2 's of these single crosses. Theoretical advanced-generation yields were calculated for combinations involving varying numbers of the 10 inbred parents. It was concluded that the most efficient number of lines would vary with the range in combining ability among the inbreds available as parents. With this particular group of 10 lines, the highest calculated

synthetic yield was obtained when only the 4 to 6 best combining lines were used. It was suggested that combinations of tested S_1 lines might be expected to produce higher yielding synthetics than more highly inbred lines having the same general combining ability.

Somewhat more critical data bearing on synthetics have been presented by Hayes, Rinke, and Tsiang (1944) and Lonnquist (1949). In the study reported by Hayes *et al.* all possible combinations among 20 lines were evaluated for performance. The 8 lines having the highest general combining ability were chosen and a synthetic produced in an isolated planting of the 28 possible single-cross combinations. This mixture was propagated under isolation by open pollination with a minimum of selection. This synthetic was compared with a standard double cross and open-pollinated variety for a three-year period. The average yield of the synthetic was superior to that of either the double cross or the variety.

Lonnquist (1949) has reported data on the performance of the second and third generations of a synthetic formed from 8 tested S_1 lines. In both generations of the synthetic yields were substantially higher than those of the original parent variety.

IX. Recurrent Selection

Any breeding scheme which involves a rapid fixation of genes imposes very definite restrictions upon the effectiveness of any selection which may be practiced. These limitations may be considered under four subdivisions (Lindstrom, 1939):

1. Large numbers of genes.
2. Masking effects of environment.
3. Complicated system of gene interaction.
4. Inadequate methods of isolating and evaluating lines.

There is no definite information on the number of genes influencing yield of grain in corn, but the consensus is that the number is large. Student (1934) has estimated that oil percentage of the corn kernel is conditioned by probably 20 to 40 genes. If no more than this minimum of genes were involved in yield and if one were dealing with a population heterozygous for these 20 genes, it would require an area of approximately 90 million acres to grow a population of sufficient size to have an even chance for the occurrence of an individual homozygous for the 20 dominant alleles. Linkage would impose still additional restrictions. The detection of a completely dominant individual, if it did occur, would also pose insurmountable difficulties. Therefore, in populations of a size which it is feasible for the breeder to handle, the opportunity for detecting individuals which surpass the mean of the

population by more than 2 or 3 standard deviation units is rather remote. A point is soon reached where an increase in population size cannot be expected to yield commensurate returns. The only solution therefore is some system which provides an opportunity for a gradual increase in the level of desirability of the populations to be sampled.

The importance of the masking effect of environment as a limitation to selection on a single plant basis requires no elaboration. Data were summarized in Section VI indicating that the masking effect of environment is very important even when one is dealing with replicated tests.

Very little is known as to the types of gene action and interaction which are involved in the determination of yield or other attributes necessary or desirable in commercial corn hybrids. There appears to be no logical reason to assume that the types of gene action and interaction are any less complex for the quantitative or heterotic effects of interest than for the qualitative characters which have been much more extensively studied. The limited information on types of gene action will be reviewed in Section X.

The remainder of this section will be devoted to the discussion of a breeding scheme which offers some opportunity of minimizing the disadvantages which are inherent in the breeding systems so far considered. This system is now designated by the general title of recurrent selection. A simplified version of this system was suggested by Jenkins (1940), and a modified version applicable to specific combining ability suggested by Hull (1945).

It is convenient to recognize four different types of recurrent selection, since they differ somewhat in procedures and assumptions with respect to the importance of different types of gene action. These are: (1) recurrent selection, (2) recurrent selection for general combining ability, (3) recurrent selection for specific combining ability, and (4) reciprocal recurrent selection. Simple recurrent selection does not require the production of test-cross progeny. The remaining three types all involve the use of a tester to measure combining ability. Different types of testers are required for methods 2, 3, and 4 because of the implied assumptions with respect to gene action. Excluding the differences introduced by the presence or absence of a tester, the four different types of recurrent selection are quite similar from an operational standpoint. Plants from a heterozygous source are self-pollinated to maintain their gene frequency and are evaluated for the desired attribute. Selfed seed of the small sample exhibiting superior performance is then planted ear-to-row. All possible intercrosses are then made by hand, or some type of bulk pollination may be used. The resulting

intercross population then serves as source material for a repetition of the selection process. Changes in gene frequency per cycle may be limited, but opportunity is afforded for cumulative selection.

1. Recurrent Selection

Recurrent selection appears to be applicable to all situations in which a reasonably accurate phenotypic evaluation is possible. It is being used for such widely diverse attributes as oil percentage of the corn kernel, the amino acids tryptophan and lysine involved in protein quality, popping expansion, and disease and insect resistance. In every case where sufficient data have been accumulated to provide a fair basis for evaluation the method appears to be highly effective. The first reports bearing on the effectiveness of the method involved selection for increased oil percentage of the corn kernel.

Sprague and Brimhall (1950) and Sprague, Miller, and Brimhall (1952) have presented data contrasting the relative effectiveness of recurrent selection and standard inbreeding with selection in increasing oil percentage of the grain. The two reports deal with material of quite unrelated origin. In each series a number of self-pollinated ears were analyzed for oil percentage. Ten ears exhibiting a high percentage of oil were chosen as foundation material for evaluating the two contrasting breeding systems. In the selfing series a progeny row was grown from each of the 10 ears. The more desirable appearing plants were self-pollinated. Approximately 5 ears were saved at harvest and each ear analyzed for oil percentage. The 2 ears of each family having the highest oil percentage were retained for further inbreeding and selection. When analytical data were available for their progeny, the sibling progeny having the lowest average oil percentage was discarded. The 2 selfed ears in the selected sibling were used to continue the family. Inbreeding and selection were continued in this manner through the S_5 generation.

In the recurrent series a second ear-to-row progeny planting was made for each of the 10 parent ears. All possible intercrosses were made by hand and the resulting intercross population used as a source material for a repetition of the selfing, evaluation, and intercrossing cycle. An effort was made to keep the land area, number of pollinations, and number of chemical analyses essentially constant for the two contrasting schemes. Any difference in results, therefore, should provide a direct measure of relative efficiency.

The results obtained from the two unrelated populations are in essential agreement in indicating that recurrent selection was superior to the standard inbreeding and selection by a factor of 2 to 5. Even

with this marked advantage the effectiveness of recurrent selection is certainly underestimated. Genetic variability in the selfing series was largely exhausted after five generations of selfing. In the recurrent series there was evidence of only a slight reduction in variability, indicating that additional repetitions of the cycle would be effective. Unpublished data have confirmed these suppositions. The marked superiority of recurrent selection appears to lie in the less rapid fixation of genes, thus offering greater opportunity for selection.

Jenkins *et al.* (1954) have reported on experiments designed to measure the efficiency of recurrent selection in concentrating genes for resistance to the leaf blight of corn caused by *Helminthosporium turcicum*. Nine single crosses involving 11 different inbred lines were used in the study. Most of the crosses represented combinations between resistant and susceptible lines. Recurrent selection was begun in most cases after two generations of backcrossing to the susceptible (Corn Belt) parent. In a few cases recurrent selection was begun after one generation of selfing or one generation of backcrossing.

Three cycles of recurrent selection were practiced within each of the 9 progeny groups, providing a total of 27 comparisons. In 24 of these comparisons the differences between successive cycles were positive, indicating an increase in resistance. In 19 of these 24 comparisons the differences were significant at either the 1 or 5 per cent level. In 3 cases the differences were negative, indicating an increase in susceptibility. The plants chosen as parents for each cycle were chosen at the time of pollination before the epiphytotic was well established. The occasional misclassification of plants may provide a partial explanation for some of the negative differences.

The results obtained suggest that two cycles of recurrent selection would be warranted in most of the groups studied. The effectiveness of the third cycle appeared to be related to progress in previous two cycles. If the gain had been substantial, little additional progress was achieved.

The results reported by Jenkins *et al.* (1954) are not in complete agreement with the results on oil percentage reported by Sprague and Brimhall (1950) and Sprague *et al.* (1952). The apparent difference in genetic variability in these contrasts may be due to: (1) a smaller number of genes determining blight resistance than oil percentage; and (2) the reduced genetic variability caused by selfing or backcrossing in the *Helminthosporium* experiment before recurrent selection was initiated.

2. Recurrent Selection for General Combining Ability

This system of recurrent selection is characterized by the continued use of a relatively stable heterozygous population as a tester parent.

Thus variations in performance among a group of test crosses would be due primarily to differences in general combining ability. Critical information on the effectiveness of this breeding method is rather limited. In the Iowa co-operative breeding program recurrent selection was a logical outgrowth of, and followed shortly after, the preliminary work on early testing.

Sprague and Brimhall (1950) have presented data suggesting that one cycle of recurrent selection was effective in increasing the average yield by about 7 bushels per acre relative to the performance of the tester parent.

Lonnquist (1951) has presented data on a single cycle of recurrent selection. High- and low-yield synthetics were available from earlier studies (Lonnquist, 1949) which had been produced by the interpolation of tested S_1 progenies. Both synthetics were sampled using the single cross WF9 $\times$ M14 as tester. The mean of the test crosses of 152 S_0 plants drawn from the high-yield synthetic was 2.7 bushels less than that of the tester and 6.4 bushels more than the test-cross yields of the S_1 line used to form the synthetic. The mean test-cross yields of 77 S_0 plants drawn from the low-yield synthetic population was 14.5 bushels less than the yield of the tester parent. Thus the original tests of S_1 progeny had been effective in separating the population into two distinct subgroups. Additional tests of S_0 plants drawn from the high-yield synthetic identified plants which were materially higher in combining ability than the S_1 progenies used to form the synthetic.

3. Recurrent Selection for Specific Combining Ability

As mentioned earlier this modification of recurrent selection was described by Hull (1945). The appropriate tester, to achieve maximum efficiency, would be a stable inbred line. No data have been published on the effectiveness of this method. Unpublished data indicate that in each of two open-pollinated varieties, using the inbred Hy as tester, yield increases of approximately 5 bushels per acre were obtained with a single cycle of selection.

This type of recurrent selection suffers from the disadvantage (Section VI) that the use of homozygous testers tends to increase the test-cross $\times$ location or test-cross $\times$ year interaction. Thus a greater amount of testing would be required for a given degree of precision than would be true for either recurrent selection for general combining ability or reciprocal recurrent selection. Another possible theoretical disadvantage may be mentioned. Inbred lines, which may currently be of importance in a breeding program, may be discarded because of the availability of newer and better lines. If an older line were involved as a tester in a recurrent selection system it might be retained in the breeding pro-

gram for a longer period than its merit justified, rather than sacrifice the effort expended in developing a specific counterpart. This difficulty may be overcome to some extent by the use of a single-cross tester. However, this would be accompanied by some reduction in efficiency of selection.

4. *Reciprocal Recurrent Selection*

This type of recurrent selection was proposed by Comstock, Robinson, and Harvey (1949). The normal procedure for the evaluation of lines begins with tests for general combining ability and proceeds to tests of specific combining ability. Any procedure which could be used to select for both general and specific combining ability during the development of lines would have obvious theoretical advantages.

The scheme proposed by Comstock *et al.* (1949) involves two foundation sources, *A* and *B*. A number of plants in source *A* are self-pollinated and outcrossed to a sample of plants of source *B*. Similarly plants from source *B* are self-pollinated and outcrossed to *A*. The two sets of test crosses are evaluated the following season. On the basis of test-cross performance the superior entries in each test are identified. Remnant selfed seed of the tested superior plants is grown on an ear-to-row basis. All possible intercrosses are then made among lines from source *A* and among lines from source *B*. These intercross populations *A'* and *B'* then serve as source material for a repetition of the cycle. The method therefore provides for selection on the basis of general combining ability and for specific combining ability when and if this becomes of importance.

No critical data are yet available for the evaluation of this breeding system. On theoretical ground, Comstock, Robinson, and Harvey (1949) have contrasted three types of recurrent selection: general combining ability using at least two single crosses as testers, specific combining ability using an inbred line or single cross as tester, and reciprocal recurrent selection, which provides for a continued and complementary change in the two populations involved. Their conclusions were that under no conditions would reciprocal recurrent selection be more than slightly inferior to the better of the other two procedures. It would be definitely superior to selection for general combining ability for all loci exhibiting overdominance or a pseudo-overdominance arising from closely linked genes in the repulsion phase. The method would also be superior to selection for specific combining ability for all loci involving partial dominance.

Each of these recurrent selection schemes poses a number of questions for which adequate answers are not yet available. How long may

recurrent selection be continued profitably? We have no information on either the gene frequency of the original population or the change in gene frequency effected by one cycle of selection. In a relatively simply inherited character such as oil, five cycles of recurrent selection have not led to a marked decrease in variability. However, this may be a favorable case, since oil percentage is little influenced by environment. What proportion of the population should be saved in each cycle? Any answer to this question must represent a compromise. The smaller the sample saved, the greater will be the genetic gain in that particular cycle. However, a small sample increases the rate of inbreeding and therefore rapidly exhausts genetic variability. In most instances one would be interested primarily in total possible gain rather than gain in any given cycle. Therefore, it appears necessary to insure a low percentage of inbreeding per cycle. Possibly 10 may be considered as an adequate number of lines to save per cycle. If all lines of the preceding cycle are equally represented in the currently selected sample, this will give a minimum rate of inbreeding of 2.8 per cent per cycle (Sprague, Miller, and Brimhall, 1952).

X. Types of Gene Action

Knowledge concerning the various types of gene action and their relative importance in determining the various attributes of interest to the breeder, is basic to the maximum efficiency of a breeding program. Unfortunately, critical information of this sort is quite inadequate. Standard breeding and testing procedures have been effective in establishing hybrid corn on a firm economic foundation. However it does not necessarily follow that this is conclusive proof of the efficiency of the procedures used.

The standard testing procedure begins with a top-cross evaluation which provides a measure of additive effects. The top-cross test is followed by single or three-way test crossing and finally by double-cross prediction and evaluation. The necessity for these later tests rests upon the existence of important nonadditive gene effects. The nature of these nonadditive gene effects is highly controversial; presumably the nonadditive effects may result from dominance, epistasis, genotype environmental interaction, and possibly other, still unrecognized sources.

Richey and Sprague (1931) and Murphy (1942) have presented data obtained from studies on convergent improvement which have a direct bearing on gene action conditioning yield of grain. Convergent improvement involves the reciprocal addition to each of two inbred lines of the dominant favorable genes lacking in one parent and present in the other. This is accomplished by selection during successive gen-

erations of backcrossing to the recurrent parent. The operations are performed in parallel, with each of the original lines serving as the recurrent parent. After a number of generations of backcrossing selected plants are self-pollinated to fix the dominant favorable genes retained from the nonrecurrent parent. As a result of this procedure new lines $A(b)$ and $B(a)$ are produced which are similar to the original lines A and B respectively, but which also possess gene substitution from the nonrecurrent parent. To the extent that this is true the lines $A(b)$ and $B(a)$ are less dissimilar than were the original lines A and B . If dominant favorable factors were responsible for the yield heterosis exhibited by the F_1 cross ($A \times B$), then certain combinations of $A(b)$ and $B(a)$ should equal the original hybrid in yield. The results obtained indicated that some of the lines $A(b)$ and $B(a)$ and some of the ($Ab \times Ba$) hybrids were actually superior to the original material. It was concluded that at least a part of the yield heterosis observed was due to the action of dominant favorable factors. Successive repetitions of the convergent improvement process would be expected to throw further light on this problem.

Crow (1948) has suggested that in crosses involving random-breeding populations, increases in vigor much greater than 5 per cent cannot be accounted for satisfactorily on the dominance hypothesis. In brief, the argument is as follows: in a random breeding population, which is at equilibrium, the frequency of a homozygous recessive is q^2 . This frequency is equal to u/s , where u equals the mutation rate and s the selective disadvantage of the allele in question. The reduction in selective value to the population because of this factor will be the product of the selective disadvantage and the proportion of individuals possessing this factor or $(s)(u/s)$. Therefore the reduction in selective value due to an undesirable recessive is equal to the mutation rate, u , of that factor. Assuming that corn possess a haploid loci number of about $n = 5000$ and an average mutation rate of approximately 10^{-5} , the product $\bar{u}$ would not be expected to be much greater than 5 per cent. In this connection it is interesting to note that of the 244 varietal comparisons summarized by Richey (1922) 17.6 per cent produced yields below the average of the two parents. Of the hybrids producing yields greater than the average of the parents, 20.6 per cent and 24.6 per cent exceeded the average yield of the two parents by percentages of 0 to 5 and 6 to 15, respectively. The great majority of the present-day commercial hybrids involve lines isolated from dent varieties. If the varietal hybrid comparisons are limited to dent $\times$ dent combinations, then the number exceeding the postulated 5 per cent would be small. Expectations under Crow's postulates therefore are in reasonably good agree-

ment with data on varietal hybrids. It may be well to emphasize at this point that the superiority of present-day hybrids is the result of a higher average yield per plant than would be obtained from open-pollinated varieties grown under the same conditions. However the best of the hybrids are not superior to the highest yielding plants which occur in an open-pollinated variety.

A much more important question is whether or not the dominance hypothesis will account for the inbreeding depression observed during the development of lines and the increased vigor expressed in the best of the hybrids between inbred lines. Crow (1948) concludes that the dominance hypothesis “. . . may explain a major part of the loss of vigor with close inbreeding of normally random mating strains and its recovery on crossing.” However, he states further that the dominance hypothesis “. . . cannot account for increase in vigor following the crossing of artificially inbred strains much beyond the level of the equilibrium population from which the inbred strains were derived.” Since the best of the present commercial hybrids exceed this level by a minimum estimate of at least 30 per cent, it appears desirable to explore other possible explanations for the observed vigor.

There are very few convincing data to indicate that the commonly observed deleterious factors have any appreciable effect on yield. Wentz and Goodsell (1929) compared yield and the frequencies of seed, seedling, and mature plant recessives in 19 varieties of corn. No significant relation was observed between yield and the number or types of defects observed. Garber and Rowley (1927) and Mangelsdorf (1928) have demonstrated that plants heterozygous for a factor conditioning defective seed (*de*) were but slightly inferior to the homozygous dominant type. Jones (1945) and Singleton (1943) have described cases of what were considered to be single-gene heterosis. In a later report, however, Jones (1952) has stated that at least some of these cannot be considered as due to a single gene. Woodworth (1931) presented data on the effect of eliminating deleterious seed, seedling, and mature plant recessives on the yields of three open-pollinated varieties. One of these, STATION REID, had been maintained by careful mass selection. A large number of vigorous healthy plants were self-pollinated and the resulting progeny classified for seed, seedling, and mature plant segregations. Selfed-ears which exhibited no segregation for deleterious recessives were composited to form a new strain, RECONSTITUTED REID. The RECONSTITUTED and original strain when compared in yield trials were found to produce approximately equal yields. However, when a large number of self-pollinated ears were obtained from the RECONSTITUTED REID it was found that a much larger percentage of the

progenies exhibited segregations for deleterious recessives than was true of the original sampling of the REID variety. If the original variety was at equilibrium, then accumulation of new mutations should approach the original value as an asymptote. Since these results were not obtained, it raises a question as to the stability of equilibrium of varieties maintained under open pollination accompanied by mass selection.

East (1936) has presented arguments for considering that the heterozygote is superior to either homozygote. Hull (1945, 1946) believes that the superiority of the heterozygote is the general situation in corn and has suggested the term "overdominance" to describe this condition. The method of recurrent selection for specific combining ability was designed to provide maximum efficiency where overdominance is of importance. Hull's conclusions as to the importance of overdominance have been drawn from several sources; the one source which has aroused the most interest has been a type of analysis involving the regression of the yield of F_1 on the yields of the parent lines. A small sample of inbred lines are usually made up into all or nearly all possible crosses for testing purposes. Where comparable yield information is available for the inbred parents, partial regressions (bp) may be calculated for each series of crosses having a common parent. A second-order regression (b_2) may then be calculated for the regression of bp on P the constant parent. For the special case $bp = 0$ it is possible to estimate a value (P_c). This represents that portion of the regression surface which is level and where heritability falls to zero.

Hull (1952) has suggested that these several estimates may be interpreted in terms of gene action. Estimates of b_2 , which are negative in sign, indicate overdominance. Positive estimates of b_2 are indicative of dominance. Estimates of P_c which fall within the range of the observed P values are also indicative of overdominance. Estimates of P_c which exceed the P values are assumed to be indicative of dominance. Hull (1952) has presented results from regression analyses of 25 experiments. (In the analysis of one set of experiments inbred line yield values obtained at Iowa were used in the analyses of F_1 yields at five other locations.) Seventeen of the experiments exhibited negative regression trends and 8, positive. If the 5 experiments where comparable inbred yield data were not available are omitted, the number of experiments exhibiting negative and positive regression trends were 12 and 8, respectively. These results suggest that overdominance may be of importance but suggest also that it may not be the predominant type of gene action with all samples of lines.

Randolph (1942) has interpreted certain comparisons involving

diploid and tetraploid lines of corn as indicating that heterozygosity in itself may be responsible for much of the vigor or heterosis exhibited by hybrids. It was found that heterozygous stocks could be doubled to produce vigorous and highly fertile tetraploids. Attempts to produce tetraploids from highly inbred lines were much less successful.

Brieger (1950) has presented arguments for and against the dominance hypothesis as an explanation for the observed heterosis. His general conclusions are that: (1) no breeding system would accumulate the numbers of undesirable recessives required by the dominance hypothesis, (2) heterotic gene systems are much superior to systems based on undesirable recessives, and (3) the dominance hypothesis is not adequate to account for the observed inbreeding results. He also contrasts two breeding systems which he designates by the terms "hybrid corn technique" and "balanced population techniques." He assumes that the "hybrid corn technique" has been successful in the United States because of the hybrid origin of our open-pollinated varieties and would be unsuccessful in other areas where the open-pollinated varieties had not arisen from the intercrossing of flint-dent types. This conclusion is not in agreement with results obtained at the São Paulo and Minas Gerais Stations in Brazil. The first hybrids developed by and released from these stations exhibit about the same superiority over native varieties as was true for the first hybrids grown in the United States.

The "balanced population technique" is essentially a system of developing synthetic varieties. However, the procedures suggested differ from those commonly used in one important respect. Instead of selecting the most vigorous material during inbreeding, selection is for weak lines, i.e., lines which are relatively intolerant of inbreeding. It is assumed that such lines will represent the homozygous condition of such heterotic alleles as are necessary for the maximum heterosis in the final synthetic or balanced population. He states that such balanced populations have been developed but presents no critical data on their performance. The use of low-yielding lines (see Section VIII) would have a depressing effect on the yield of any synthetics produced.

Comstock and Robinson (1948) have outlined procedures for estimating heritability and degree of dominance, and Robinson, Comstock, and Harvey (1949) have presented data for a number of attributes. Briefly the method consists in making a series of "biparental" crosses within an F_2 single-cross population. The crosses are grown in replicated plots and individual plant measurement taken for a number of attributes. Estimates of variance components may then be calculated for "males in sets," "females in sets," and "males $\times$ females in sets." The various components may then be used to calculate a term " α "

which is the average degree of dominance. If " a " = 1, complete dominance is indicated; if $a > 1$, overdominance; and if $a < 1$, partial dominance. The data presented by Robinson, Comstock, and Harvey (1949) indicate " a " values closely approximating 1 for husk extension and ear diameter. Estimates for plant height, husk score, ear number, and ear length indicate partial dominance. The pooled estimate of " a " for yield was 1.64, suggesting overdominance. However, the authors point out that close linkage in the repulsion phase could also lead to values in excess of 1. This estimate therefore may be considered as suggestive of the importance but not necessarily as crucial evidence for overdominance.

Gardner, Harvey, Comstock, and Robinson (1953) have also reported estimates of dominance for a series of quantitative characters. The method involves the use of a series of F_2 plants backcrossed to each of the two parental lines. Estimates of variance components are obtained for F_2 parents and the $F_2 \times$ inbred interaction. The calculated " a " values were in very good agreement with the earlier estimates of Robinson, Comstock, and Harvey (1949). In this study also dominance estimates for yield were significantly greater than 1. A method was proposed for determining the effects of close linkage in the repulsion phase through the use of a series of unselected stable lines derived from an F_2 population. In the current study, however, either close linkage in the repulsion phase or overdominance could account for the observed estimates. It should be pointed out that either of these two possibilities would have rather similar immediate consequences in a corn-breeding program, since fixation of the most vigorous type would be impossible or highly improbable.

Stringfield (1950) has presented data on a balanced series of combinations ranging from 0 to 100 per cent heterozygosity. On the basis of disparity in yield between F_2 and backcross progenies, between F_1 vs. three-way and double crosses, etc., he concludes that no one of the three assumptions, (1) cumulative action of dominants each having a small effect relative to its recessive allele, (2) strong interaction among nonallelic dominants, or (3) heterozygosis *per se*, provides an entirely adequate explanation of the results obtained.

An adequate explanation of heterosis in terms of genes and their physiological function would be highly desirable, but it appears rather unlikely of attainment in the near future. In the meantime information on the relative importance of various types of gene action would be helpful to the plant breeder. Some of the methods reviewed here offer promise of great usefulness when sufficient data are available to warrant generalization.

Another approach to this problem of the relative importance of different types of gene action has been proposed by Sprague and Miller (1950). This proposal would utilize the mechanics of recurrent selection for specific combining ability. Two heterozygous sources are crossed to a common inbred tester. If the original heterozygous populations are designated A and B , then intercross populations within each source may be designated A_1, B_1, A_2, B_2 , etc., depending upon the number of cycles selection has been practiced. If dominance is the only type of gene action involved, the high-yielding test crosses represent individuals having a greater than average number of dominants and continued cycles would lead to a gene frequency of 1.0 at the limit. Conversely if overdominance is the prime factor, then the superior individuals are those exhibiting the greatest heterozygosity when combined with the tester parent. Intercrossing and continued selection within this group would, at the limit, lead to gene frequencies of $1 - q$, if q represents the gene frequency of the inbred tester. The contrast between $A \times B, A_1 \times B_1, A_2 \times B_2$, etc., should provide information on the relative importance of dominance and overdominance. If dominance is of prime importance, the series of crosses should exhibit an increasing yield trend; whereas a decreasing yield trend would be expected if overdominance were highly important. With certain gene frequencies this method may exhibit an increasing yield trend even when overdominance is important. However, such gene frequencies are not those expected under equilibrium conditions. Only limited results are available from this method at present, and these must therefore be interpreted with caution. The data however are in agreement with expectation under the dominance hypothesis.

It is apparent from the studies which have been reviewed that no general agreement has been reached on the interpretation of heterosis. Since an adequate explanation of heterosis is one of the most important problems in corn breeding, any method which can be devised, which will contribute *critical* information, should be vigorously explored.

XI. Cytoplasmic Sterility

The use of some form of sterility to avoid the necessity for detasseling in the production of single- and double-cross seed has been an intriguing possibility through the years. Attempts by a number of workers to use gene-controlled sterility did not prove successful. The first cytoplasmic sterile stock reported (Rhoades, 1931, 1933) was obtained from a Peruvian variety collected by R. A. Emerson and F. D. Richey. In the studies reported by Rhoades (1933) it was conclusively

demonstrated that pollen sterility was controlled primarily by the cytoplasm. A systematic study of many chromosome segments failed to reveal any which had a marked effect on pollen fertility. This stock was used by Richey and Sprague (unpublished) to transfer sterility to standard lines. Strains which were completely sterile under field conditions were obtained without difficulty. However, many of these same strains were completely fertile when grown in the greenhouse. It appeared that a type exhibiting this degree of environmental response would be of limited usefulness in commercial seed production, and the studies were discontinued and the stock eventually was lost.

The second instance of cytoplasmic sterility was reported by Josephson and Jenkins (1948) and involved the long-time inbred white line, Ind. 33-16. This particular line imparts sterility only when it is used as the female parent of the female single cross. It was determined that a number of inbred lines have the ability to restore normal fertility and that at least two genes must be involved. It is apparent therefore that sterility or fertility is not a function of the cytoplasm alone but is dependent upon the cytoplasmic-genotypic interaction.

Three other types of cytoplasmic sterility have received some attention. One of these, described by Jones (1950, 1951) and Gabelman (1949), originated from a cross involving the genetic type "Ioja." In the 1950 paper Jones assumed he was working with the sterile type reported by Rhoades (1931). However, the seed used had been obtained from Jenkins, who states it was of Ioja origin.

In this strain Gabelman (1949) has reported that sterility has a particulate basis. The presence of one or more of these cytoplasmic particles in the microspore results in the failure of normal pollen development. Jones (1950) and Jones and Mangelsdorf (1951) found that certain lines have the ability to restore fertility and that fertility restoration appears to be conditioned by a single dominant gene.

Rhoades (1943, 1950) has presented evidence that crosses involving the "Ioja" gene often give rise to plants exhibiting cytoplasmic male sterility. Whether these spontaneously arising cases represent distinctly different types or are merely recurrences of a single basic type has not been completely established.

A cytoplasmic male-sterile stock of different origin has been reported by Rogers and Edwardson (1952). A number of sterile types have been found in the Mexican June strains. The particular source which has been studied most extensively occurred as a mutation in an inbred line of Golden June. A number of inbred lines have been crossed on to this sterile source. F_1 hybrids of some of the combinations are completely sterile, others may exhibit partial or complete fertility. Un-

published results from several workers suggest that fertility restoration may be due to a single dominant gene. Rogers and Edwardson (1952) and Jones and Everett (1949) have suggested that inbred lines carrying fertility-restoring genes may be used as the male parent of the double cross and thus insure complete fertility in the commercial crop.

A cytoplasmic male-sterile type described by Schwartz (1951a, 1951b) apparently has a genetic basis quite different from that of the types previously mentioned. This type of sterility is dependent upon a specific cytoplasm $\square$, a dominant gene ($Ms21$) for sterility and a dominant suppressor S^{Ga} associated with a gametophyte effect. The male-sterile plants have the genotype $\square Ms ms s^{Ga} s^{Ga}$. Owing to selective fertilization s^{Ga} is either not transmitted through the male or transmitted with very low frequency. All of the lines which have been tested, with the exception of *Kys*, which was involved in the original cross in which the sterility was detected, are homozygous for the S^{Ga} allele. Thus any inbred line has the ability to restore fertility. This would be a decided advantage in the commercial utilization of this form of sterility. This theoretical advantage, however, is largely nullified by the inability to recover s^{Ga} gametes from the pollen of heterozygous plants.

More recent studies conducted at the Illinois Station (unpublished) raise the question as to whether this type of sterility actually has a cytoplasmic basis. If a cytoplasmic basis is lacking, this sterility mechanism is entirely genetic and such types have in the past been found unsatisfactory. Until these opposing conclusions have been reconciled the *Kys* sterile source should receive little attention from commercial seedsmen.

The Texas and Iojap sterility sources are currently being used in the production of commercial hybrid seed. Hybrids are now being produced with the Texas source in which one line of the male single cross carries the fertility-restoring factor. Thus approximately half of the plants in commercial plantings are fully fertile. This appears to provide sufficient pollen for satisfactory seed set.

Pollen fertility-restoring lines are not in general use as yet with the Iojap type of sterility. Therefore the commercial utilization of this sterile source requires the production and blending of two similar double crosses, one completely fertile and the second completely sterile. Blending may be accomplished by planting 4 rows of the sterile female single cross and 2 rows of its fertile counterpart within each 6-row block of female rows of the double-crossing field or by mixing of the two types of double cross seed produced in separate fields. As the fertile rows are detasseled the supposedly sterile rows must be checked for the presence

of undesired fertile plants. Any such plants found must be detasseled before pollen shedding begins, to avoid contamination. No distinction between fertile and sterile rows is made at harvest time. The operations involved in harvesting, drying, shelling, and sizing are done with the bulked seed, and it is the general feeling that this will produce a satisfactory blending of the two types. This may not prove to be adequate in all cases (see Chapter IX).

The use of male sterility to avoid detasseling is a procedure of primary interest to the seed producer. The farmer need not be concerned as to whether the sterility mechanism was used in seed production if he can be assured of the performance and adaptability of the resulting hybrid. The use of cytoplasmic male sterility will undoubtedly increase as work progresses on the introduction of the cytoplasmic and pollen fertility restoration systems into more of the widely used lines.

The dependence of the hybrid corn industry on cytoplasmic sterility to avoid detasseling may have at least one important drawback. The time required for the development and evaluation of a new hybrid combination is usually estimated at a minimum of 10 years. An additional period of several years will be required to introduce the sterility and pollen fertility restoration characteristics into new lines after their value has been proved. Unless some simpler and less time-consuming technique can be devised, the net result will be a retardation of the utilization of new and superior combinations. Such a situation would be of somewhat less importance in the Corn Belt than in other areas where the introduction of new hybrids is proceeding at a more rapid rate.

XII. Insect Resistance

Corn is subject to attacks from a large number of different insect pests. Only a few of these are present in destructive numbers in a given locality every year. The lack of regular infestations has proved to be a serious deterrent to studies on inheritance of resistance or breeding for resistance. Many of the data on resistance which have been accumulated have been on material grown for other purposes. As a result the data are often adequate to suggest differences in degree of resistance but provide little information as to the genetic basis for such differences.

Techniques have been developed for artificial infestation with the European corn borer, *Pyrausta nubilalis*, and as a result more information is available on resistance than is true of any other insect pest. The European corn borer exists in two distinct forms: univoltine and multivoltine. Arbuthnot (1944) has reported that these two types differ by a single genetic factor. The feeding habits of the young larvae of the

univoltine strain and the first brood of the multivoltine strain are quite similar. Resistance due to differential larvae survival is therefore similar for the two types. In the second brood of the multivoltine strains, the young larvae pass through the first two or three instars feeding largely on pollen rather than on leaf tissue. Under such conditions no indication of a differential rate of survival has been noted. Later instars burrow into stalk and shank in the same manner as the later instars of the univoltine strain. Strains of corn differ markedly in the degree of damage, expressed as broken stalks, dropped ears, etc., resulting from a given degree of borer infestation. These differences in damage are designated as differences in tolerance and may result from attacks of the univoltine strain or the second or later generations of the multivoltine strain. Differences in resistance are related to differential survival of the early instars of the univoltine strain or the first generation of the multivoltine strain where feeding is confined largely to leaf blade tissue.

Strains of corn also exhibit a differential attractiveness to moths at the time of oviposition. The basis for this differential attractiveness is unknown, but it is at least partly hereditary. Single crosses involving preferred lines receive a larger number of egg masses than single crosses involving avoided or nonpreferred lines. However, these differences are thought to be of little importance, since moths will lay the normal number of eggs on nonpreferred lines when no choice is available. Myers *et al.* (1937) presented the first detailed report on resistance and the problems involved in its evaluation. Differential resistance to survival and establishment has received major emphasis because of the feasibility of hand infestation with egg masses. Patch (1943) and Patch and Everly (1945) have presented data indicating that differences in survival may be apparent within a few days after hatching. Borers which do survive develop at a slower rate in the resistant strain. It is assumed that these differences in survival and establishment are related to nutritional inadequacies of the resistant lines. No evidence is available at present as to the substance or substances involved.

Resistance appears to be conditioned by multiple factors. As a result of extensive hand infestation a large number of lines are now available having a satisfactory degree of resistance to the European corn borer. General observation indicates that resistance of double-cross hybrids is related to the resistance of the inbred parents. As the relative resistance of individual parent lines or as the number of such lines increases, the resistance of the hybrid increases accordingly. Relatively few resistant hybrids are now in commercial production.

Inbred strains and hybrids also differ markedly in tolerance to

borer damage as measured by stalk breaking at maturity. In general, the tolerant strains are those which exhibit the greatest resistance to stalk rots in the absence of the borer. On the basis of information now available it appears quite feasible to combine both resistance and tolerance.

Artificial infestation techniques have also been developed for the corn earworm, *Heliothis armigera*, which regularly does some damage to the corn crop. Kyle (1918) reported that selection for long husk extension reduced damage from corn earworm and also black weevils (*Sitophilus oryza*). Collins and Kempton (1917) reported that interprogeny correlation between husk extension and earworm damage was -0.71 . Husk extension as a factor in resistance was also emphasized by Phillips and Barber (1931). Painter and Brunson (1940), Blanchard, Bigger, and Snelling (1941), Richey (1944), and Dicke and Jenkins (1945) have presented evidence that certain inbred lines regularly contribute resistance to earworm attack to their hybrids. This resistance is not due solely to tightness of husk and husk extension. Painter and Brunson (1940) and Richey (1944) noted that lines and crosses differed in susceptibility to leaf or "bud" feeding by the corn-ear worm. Resistance appears to be conditioned by multiple factors, but Richey (1944) reports an indication of a major gene for resistance on the 6th chromosome.

Methods have been developed for artificially infesting ear shoots with young corn-ear worm larvae. It has been demonstrated that certain strains do not provide favorable environment or nutrition for the development of the young larvae. This condition has been called "silk lethal," and is subject to genetic control.

The southern corn rootworm, *Diabrotica undecimpunctata*, and the corn rootworm, *D. longicornis*, do considerable damage in some seasons and under some conditions. Bigger, Holbert, Flint, and Lang (1938) have reported that inbred strains and hybrids differ in tolerance to the root-feeding larvae of the southern corn rootworm. This tolerance appears to lie in the rapidity of regeneration of a new root system rather than differential feeding. Routine ratings for difference in tolerance to either of the above species is complicated by the irregularity of distribution. Attacks may be extremely severe in small areas, and little or no damage be apparent in other spots only a few feet away.

Chinch bugs, *Blissus leucopterus*, may cause very severe damage in some years. Heavy infestations are dependent upon favorable weather conditions for overwintering and for development of the first brood. This brood normally starts its development on small grain and migrates to corn as the small grains ripen. Infestation, during migration, is so

heavy that significant differences in resistance have not been observed. The second generation (winged form) does not attain the same population density, and differential resistance has been reported. Flint and Hackleman (1923) observed that certain open-pollinated varieties, which were then grown in southern Illinois, possessed considerable resistance to attacks of the second-generation form. Holbert, Flint, Bigger, and Dungan (1935) and Snelling and Dahms (1937) have presented additional information on the differential resistance of both open-pollinated varieties and double-cross hybrids.

Brunson and Painter (1938) reported differential feeding by grasshoppers (*Melanoplus differentialis* and *M. bivittatus*). Estimated defoliation for a group of varieties ranged from 7.6 to 31.4 per cent and for a group of double crosses from 4.0 to 59.8 per cent.

Under severe infestation, leaf aphids (*Aphis maidis*) may cause low yields owing to the combined effect of poor pollination and direct feeding injury. McColloch (1921) has reported differences among varieties in resistance to leaf aphids. Walter and Brunson (1940) and Snelling, Blanchard, and Bigger (1940) have reported that inbred lines exhibit marked differences in resistance. F_1 crosses between resistant lines tend also to be resistant. Huber and Stringfield (1942) have also reported difference in resistance among both inbred lines and hybrids. They report also that aphid susceptibility was significantly correlated with damage caused by the European corn borer. They suggest that this association is sufficiently close that aphid resistance may be used to predict resistance to the corn borer. Walter and Brunson (1946) practiced selection for aphid resistance in three long-time self-fertilized lines. Evidence was presented indicating that selection appeared to be effective in some lines and rather ineffective in others.

Hoegemeyer (1941) has reported differential root injury and lodging due to white grubs (*Phyllophaga* spp.). Both single and double crosses were under observation, and it was observed that the single crosses exhibiting the least root injury tended to transmit this superiority to their double-cross progeny.

XIII. Disease Resistance

Corn is subject to attack by a large number of disease organisms. The important diseases are discussed in some detail in Chapter XII. In this section we shall be concerned only with information on differential resistance and its genetic basis where known.

A number of different genera cause root rotting in corn. Of this group *Pythium* is the only genus which is primarily a root-rotting

organism. Some species of *Pythium* are more pathogenic under the conditions prevailing during later stages of growth. A differential in ability to germinate under "cold-test" conditions has been reported by a number of workers. In many of these studies, however, the organism or organisms inciting seed and seedling rot were not identified. Tatum (1942) and Pinnell (1949) reported that there were large differences among inbred lines in their ability to germinate under cold-test conditions. These differences appeared to have a genetic basis, since significant correlations were obtained between response of the maternal inbred parent and the single cross. A pronounced maternal effect was observed in most crosses. Variability in response within a given genotype was quite marked. Livingston (1951) and Rush and Neal (1951) reported that maturity at time of harvest were important factors affecting cold-test response. Tatum (1942) and Wortman and Rinke (1951) emphasized the importance of pericarp damage as a factor influencing cold-test response. Hooker and Dickson (1952) have suggested the use of excised corn embryos for measuring resistance to *Pythium* under low-temperature conditions. Data were presented indicating that this technique eliminated a considerable part of the variation in response reported by other workers. Even with the use of excised embryos there was evidence of a maternal effect. These workers conclude that genotypic differences among embryos determine the major course of seedling reaction to *Pythium* at low temperatures.

A limited number of studies on resistance to other seedling blights have been reported. McIndoe (1931) working with *Giberella saubinetii* found marked differences in resistance among the material tested and concluded that resistance was conditioned by multiple factors. Hayes, Johnson, and Stakman (1933) working with later generations of the same material found little correlation between the reaction of F_3 and F_4 lines.

An artificial inoculation technique for measuring resistance to stalk rots has been available for several years. This method is now widely used in the evaluation of new inbred lines. Smith, Hoppe, and Holbert (1938) reported a comparison of the incidence of *Diplodia* stalk rot under natural infection and artificial inoculation. The correlation between natural infection and broken stalks was $+0.909$. The correlations between natural infection and cortical spread or pith spread (artificial inoculation) were $+0.853$ and $+0.878$, respectively. It was concluded that relative resistance to *Diplodia* stalk rot could be measured by means of artificial inoculation. As a result of these and other studies the inoculation of material during the early stages of inbreeding has become a routine procedure. In some cases *Diplodia* is used as the stalk-

rotting organism. Other workers use a mixture of several genera for routine inoculations.

Inoculation techniques for evaluating differential resistance to ear rots have not been too successful. Under conditions of heavy natural infestation some differences in degree of resistance have been noted. Smith and Madsen (1949) report marked variation among the 60 dent lines evaluated for *Fusarium* ear rot susceptibility. Sixteen of the lines were classified as possessing sufficient resistance to be useful under California conditions.

Inoculation techniques have been tried with both *Diplodia* and *Gibberella*, but it has been difficult to standardize procedures to insure a sufficiently light infestation to provide a satisfactory differential.

Leaf blights may be caused by a number of different genera. However, species of *Helminthosporium* and *Bacterium stewartii* appear to be of most importance. At least three species of *Helminthosporium* are known to parasitize corn. These are *H. turcicum* (Northern leaf blight), *H. maydis* (Southern leaf blight), and *H. carbonum*. The latter may cause both a leaf blight and an ear rot.

Ullstrup (1944) has reported two physiologic races of *H. carbonum*. Resistance to race 1 has been shown to be inherited as a monogenic dominant located on chromosome 1 (Ullstrup and Brunson, 1947, Roman and Ullstrup, 1951). Jenkins and Robert (1952) and Jenkins, Robert, and Findley (1952) have reported on resistance to leaf blight caused by *Helminthosporium turcicum*. It was concluded that resistance is controlled by many genes. However, there was evidence for a few genes with major effects. Elliott and Jenkins (1946) have demonstrated that large differences in degree of resistance exist among inbred lines and crosses and unpublished work by both Jenkins and Ullstrup shows that a satisfactory degree of resistance can be transferred by a back-crossing technique. Inheritance studies with *H. maydis* have not been reported. However information is available indicating that certain lines possess a rather high degree of resistance and that this resistance can be transferred by appropriate breeding methods.

Bacterial wilt (*Bacterium stewartii*) is often destructive to sweet corn. Other types may also be attacked but normally damage is much less on later material. Wellhausen (1937) reported that resistance to this pathogen was dominant. He postulated three factor pairs, SW_1 , SW_2 , and SW_3 to account for the observed variation in degree of resistance. SW_1 produced the greatest and SW_3 the least effect when the other factors involved were present in the recessive condition. Studies also indicated that the virulence of the pathogen could readily be modified by passage through a resistant or susceptible host.

Leaf rust (*Puccinia sorghi*) is widespread and in certain years may cause reductions in yield. Stakman, Christensen, and Brewbaker (1928) have reported seven physiologic races. The differential hosts used have not been maintained, and no recent studies on specialization in this rust have been reported. Rhoades (1935), using X-ray induced deficiencies, found that the factor conditioning resistance to race 3 was located in the short arm of chromosome 10.

In the United States two different organisms may produce smut on corn. These are common smut (*Ustilago maydis*) and head smut (*Spacelotheca reiliana*). Of these *Ustilago maydis* is the more common and destructive. All of the studies on differential resistance and inheritance of resistance have been done with this type. Inoculation techniques have been reported but are not completely satisfactory. All of the inheritance studies have been done under conditions of natural infection.

Immer (1927) and Hoover (1932) studied the inheritance of smut resistance in crosses between inbred lines and genetic stocks representing several linkage groups. Associations were noted between susceptibility and various morphological characters such as brachytic, ramosa, liguleless, and tassel seed. In these studies there is the possibility that the morphological character may condition susceptibility to infection. This possible limitation was avoided in studies reported by Burnham and Cartledge (1939) and Saboe and Hayes (1941) by the use of translocation stocks. As far as is known chromosomal translocations produce neither morphological nor physiological aberrations which would favor the entrance of the pathogen. Burnham and Cartledge (1939) observed associations between smut reaction and point of interchange in 13 translocation strains. Saboe and Hayes (1941) used a series of translocations marking 15 arms of the 10 chromosomes. In crosses involving a smut-resistant MINN. NO. 13 line, factors for smut resistance were located on the long arms of chromosomes 7 and 8 and on the short arm of chromosome 6. In crosses involving a smut-resistant line from the variety RUSTLER, factors for resistance were indicated in the long arm of either chromosome 8 or 5. On the basis of these results it was concluded that smut resistance in the two lines was conditioned by different genes.

The limited amount of work which has been done on disease resistance in corn is largely a consequence of inadequate inoculation techniques for many of the important diseases. The losses from plant diseases are sufficiently great to justify much greater emphasis on the development of suitable techniques and thereby facilitate the development of resistant inbred lines and hybrids.

XIV. Chemical Composition

A breeding program designed to modify the chemical composition of corn would normally have one of two objectives, either to increase the value of corn to the industrial miller or to increase its value as food or feed. Both objectives have received attention, but somewhat more progress has been achieved with the first as judged by the acreage devoted to modified hybrids.

We shall consider first the possible modification of corn which may increase or extend its usefulness to the wet-milling industry. Corn oil is of high quality and is used extensively for food uses (Chapter XIV). It is one of the most valuable by-products from the wet milling of corn. Therefore the wet millers, as a group, would be interested in strains of corn having a higher percentage of oil than that commonly grown (4.5 to 5.0 per cent). The first extensive studies designed to increase oil percentage were reported by Winter (1929). These studies were begun in 1896 and the report by Winter summarized the first 29 years of selection. The ear-to-row breeding system was used, and selection had been practiced for both high and low oil percentage. In the high-oil strain, oil percentage was increased from 4.7 to 9.9 and in the low-oil strain oil content had decreased from 4.7 to 1.5. Woodworth, Leng, and Jugenheimer (1952) have reported on 50 years of selection in this same material. At the end of the 50-year period the high-oil strain averaged 15.36 and the low oil strain 1.01 per cent. Miller and Brimhall (1951) have presented data indicating that over the range from about 2.8 to 8.0 per cent there is no important relationship between oil percentage and yield. Woodworth and co-workers presented data indicating that high-yielding hybrids having about 6 per cent of oil can be produced. Sprague and Brimhall (1950) and Sprague, Miller, and Brimhall (1952) have shown that increased oil percentage may be achieved more efficiently by recurrent selection than by the conventional inbreeding and selection methods. The possible limitations of high-oil corn for use as a feed will be discussed later.

Starch is the main product of the wet-milling industry. Corn starch is modified in many ways to fill special industrial demands (Chapter XIV). Attempts to produce corn having starch with properties different from normal have been partially successful. One of these types is waxy corn. Brink and Abegg (1926) reported that the principal carbohydrate reserves in waxy and normal corn were different. Brimhall and Hixon (1939, 1942) and Morgan (1940) have shown that the two types of corn have quite different pasting characteristics. Hixon and Sprague (1942) interpreted these differences in terms of molecular structure.

Waxy corn starch contains only the branched molecular form, amylopectin. Starch from nonwaxy corn contains approximately 72 per cent of amylopectin and 28 per cent of the straight-chain molecular form, amylose. The development of waxy corn as a commercial crop has been described by Sprague and Jenkins (1948).

Three alleles are known for the waxy locus (Sprague, Brimhall, and Hixon, 1943; Brimhall, Sprague, and Sass 1945).

The allele conditioning normal starch, Wx , is dominant to the other two alleles as measured by either iodine reaction or amylose percentage. Gene dosage studies on viscosity characteristics of the starch pastes suggest that gene action is primarily additive. If only the two alleles wx^a and wx (characterized by high percentages of amylopectin) are considered, gene dosage studies suggest that amylose percentage follows a geometric and viscosity, an arithmetic, type of gene action.

Types of corn characterized by a high percentage of amylose would have commercial possibilities in the field of films and fibers. Genetic systems have been reported which produce increased percentages of amylose. Cameron (1947) reported on starch modifications conditioned by the genes su^{am} , su , and du . The $su\ du$ homozygote produced starch having 65 per cent of amylose, but the total starch yield was quite low. Kramer and Whistler (1949) and Dvonch, Kramer, and Whistler (1951) reported that su_2 also produced starch having a higher than normal percentage of amylose. Dunn, Kramer, and Whistler (1953) reported the interactions and dosage effects for all possible genotypes involving the genes su , su_2 , and du . Of the three simple recessives su_2 produced the greatest effect on amylose percentage. The genes su and du exhibited a marked degree of interaction, as measured by amylose percentage; this is in agreement with the earlier report by Cameron (1947). A high negative correlation was observed between per cent starch and per cent amylose in the starch. The triple recessive type su , su_2 , du produced only 9 per cent starch, but 77 per cent of this starch was amylose. It is obvious from this negative association that the genetic system, su , su_2 , du will not provide high-amylose types having commercial possibilities. It is possible, however, that other genetic systems may be found which will produce high-amylose starch in acceptable yields.

Corn as a livestock feed serves primarily as an energy source. The whole grain has poor protein quality and is deficient in certain vitamins. Obviously its value as a feed would be increased if protein quality and vitamin content were increased. Within limits an increase in energy would not be undesirable. The work which has been done in modifying chemical composition has been directed toward one of three

general aims: increased energy through an increase in oil percentage, an increase in either protein quantity or quality, and selection for increased niacin content.

An increase in the fat content of the ration has been shown to lead to increased yields of butterfat by the dairy cow. Increases in the fat content of poultry ration have also been shown to be beneficial. Ellis and Isbell (1926) have reported that increase of corn oil in the ration of swine resulted in carcasses exhibiting soft pork characteristics and lard with a low melting point. However, Brimhall and Sprague (1951) have found that as the oil percentage of corn is increased by selection there is an accompanying decrease in iodine number. Therefore, feeding increased quantities of ordinary corn oil may not provide an adequate basis for predicting the results to be expected from high-oil corn. This general problem will be discussed in more detail in Chapter XV.

An increase in oil percentage appears to be related to the general problem of improving protein quality. An increase in oil percentage is brought about mainly by an increase in germ size. Mitchell and Beadles (1944) have found the protein of corn germ to be a high-quality protein. Therefore, it has been argued that high-oil strains should be superior in protein quality. Schneider, Earley, and DeTurk (1952) have concluded that the biological value of high-oil corn is probably greater than that of low-oil corn. However zein made up about the same percentage of the total nitrogen for both types.

A number of studies have been reported which deal with the interrelations of certain amino acids, zein, niacin, and total protein. Such studies provide the basis for breeding studies designed to improve protein quality.

Frey (1949, 1951) reported that the percentages of the amino acids valine, leucine, and isoleucine were highly correlated. The correlations between tryptophan and any of the above-mentioned amino acids were in general significant but numerically smaller than those observed within the valine, etc., series. By means of a regression technique, Frey (1951) was able to establish that as protein percentage increases, zein made up an increasing percentage of the total. The same relationship was apparent for the amino acids valine, leucine, and isoleucine. The relative amounts of tryptophan decreased as the protein percentage increased. Frey, Brimhall, and Sprague (1949) found that recurrent selection based on the zein-total protein ratio was not effective. However selection based on tryptophan alone was quite effective in increasing the relative tryptophan content. Unpublished data indicate that recurrent selection for lysine percentage is also equally effective.

Miller, Hurst, and Brimhall (1952) found that lysine becomes a

decreasing proportion of the corn protein as total protein percentage increases. Flynn *et al.* (1950) reported increased percentages of lysine as the percentage of crude protein increased when both were expressed as percentages of the whole corn. However if expressed as a percentage of the protein, the per cent of lysine decreased as protein percentage increased. Miller, Aurand, and Flack (1950) reported that lysine and total protein were positively correlated in the sample of nine single crosses studied.

Breeding for improved protein quality in corn must take into consideration both of the essential amino acids tryptophan and lysine and should also recognize the value of increased percentages of niacin. Within certain limits niacin and tryptophan exhibit a mutually sparing relationship. Richey and Dawson (1948, 1951) have reported that niacin content of the corn grain is quantitative in inheritance and can readily be increased by selection. Cameron and Teas (1948) and others have demonstrated a negative relation between starch and niacin content. Miller, Hurst, and Brimhall (1952) found no important relation between niacin and total protein or any of the protein components studied. Rodriguez, Hunt, and Bethke (1950) report a small negative correlation between niacin and crude protein. Teas, Cameron, and Newton (1952) have presented data on tryptophan, niacin, and indoleacetic acid during the development of the corn kernel. Tryptophan and indoleacetic acid decreased rapidly during subsequent kernel development. Niacin increased rather gradually throughout the developmental period.

From the results which have been presented it is apparent that high-oil and improved protein quality types may be obtained by breeding. Knowledge as to upper limits which may be achieved must await more extensive studies. It is apparent, however, that breeding for improved protein quality would be less empirical if more knowledge were available on nitrogen metabolism and protein synthesis.

XV. Conclusion

As mentioned at the beginning of this chapter, corn breeding has utilized quite different methods at different periods of its recorded history. The methods now in common use, a direct outgrowth of the early work of Shull, East, and others, hold promise of continued progress. Some persons feel that with the better current hybrids a ceiling has been established and that further progress must be sought in greater disease and insect resistance, increased suitability to mechanical harvesting, etc. The writer cannot accept this viewpoint.

The claim is often made that the development and utilization of hybrid corn represents one of the great advances in agriculture of the twentieth century. With this claim there is no argument. However, corn breeding today is nearly as empirical as when Shull (1909) outlined the development and utilization of inbred lines in considerable detail. Important advances have been made since that time, but the basic problems then and now remain much the same. What is the genetic basis of heterosis, and how can it be used most efficiently in the breeding of corn? It would appear that a much greater expenditure of time and money could well be devoted to a detailed study of theoretical problems to ensure a sound basis for further developments.

REFERENCES

- ANDERSON, D. C. 1938. The relation between single and double cross yields in corn. *J. Am. Soc. Agron.* **30**: 209-211.
- ANDERSON, E., and BROWN, W. L. 1952. Origin of Corn Belt maize and its genetic significance. in "Heterosis," Chapter 8, pp. 124-148. Iowa State College Press, Ames, Iowa.
- ARBUTHNOT, K. D. 1944. Strains of the European corn borer in the United States. *U.S. Dept. Agr. Tech. Bull.* **869**, 1-20.
- BEAL, W. J. 1877. Report of the Professor of Botany and Horticulture. *Rept. Mich. Bd. Agr.*, pp. 41-59.
- BEAL, W. J. 1880. Indian Corn. *Rept. Mich. Bd. Agr.*, pp. 279-289.
- BEAL, W. J. 1881-82. Report of the Professor of Botany and Horticulture. *Rept. Mich. Bd. Agr.*, pp. 98-153.
- BEVERLY, R. 1705. The history and present state of Virginia. Printed by R. Parker, at the Unicorn under the Piazza's of the Royal Exchange.
- BIGGER, J. H., HOLBERT, J. C., FLINT, W., and LANG, A. L. 1938. Resistance of certain corn hybrids to attack of southern corn rootworm. *J. Econ. Entomol.* **31**: 102-107.
- BLANCHARD, R. A., BIGGER, J. H., and SNELLING, R. O. 1941. Resistance of corn strains to the corn ear worm. *J. Am. Soc. Agron.* **33**: 344-350.
- BRIEGER, F. G. 1950. The genetic basis of heterosis in maize. *Genetics* **35**: 420-445.
- BRIMHALL, B., and HIXON, R. M. 1939. The rigidity of starch pastes. *Ind. Eng. Chem. (Anal. Ed.)* **11**: 358-361.
- BRIMHALL, B., and HIXON, R. M. 1942. Interpretation of viscosity measurements of starch pastes. *Cereal Chem.* **19**: 425-441.
- BRIMHALL, B., and SPRAGUE, G. F. 1951. Unsaturation of corn oil—Inheritance and maturity studies. *Cereal Chem.* **28**: 225-231.
- BRIMHALL, B., SPRAGUE, G. F., and SASS, J. E. 1945. A new waxy allele in corn and its effect on the properties of the endosperm starch. *J. Am. Soc. Agron.* **37**: 937-944.
- BRINK, R. A., and ABEGG, F. A. 1926. Dynamics of the waxy gene in maize. I. The carbohydrate reserves in endosperm and pollen. *Genetics* **11**: 163-199.
- BRUNSON, A. M., and PAINTER, R. H. 1938. Differential feeding of grasshoppers on corn and sorghums. *J. Am. Soc. Agron.* **30**: 334-346.
- BURNHAM, C. R. 1946. An "Oenothera" or multiple translocation method of establishing homozygous lines. *J. Am. Soc. Agron.* **38**: 702-707.

- BURNHAM, C. R., and CARTLEDGE, J. L. 1939. Linkage relations between smut resistance and semi-sterility in maize. *J. Am. Soc. Agron.* **31**: 924-933.
- CAMERON, J. W. 1947. Chemico-genetic basis for the reserve carbohydrates in maize endosperm. *Genetics* **32**: 459-485.
- CAMERON, J. W., and TEAS, H. J. 1948. The relation between nicotinic acid and carbohydrates in a series of maize endosperm genotypes. *Proc. Natl. Acad. Sci. U.S.* **34**: 390-398.
- CHASE, S. S. 1949. Monoploid frequencies in a commercial double cross hybrid maize and in its component single cross hybrids and inbred lines. *Genetics* **34**: 328-332.
- CHASE, S. S. 1952a. Production of homozygous diploids of maize from monoploids. *Agron. J.* **44**: 263-267.
- CHASE, S. S. 1952b. Monoploids in maize. in "Heterosis," Ch. 25, 389-399. Iowa State College Press, Ames, Iowa.
- COLLINS, G. N. 1910. The value of first generation hybrids in corn. *U.S. Dept. Agr. Bur. Plant Ind. Bull.* **191**, 1-45.
- COLLINS, G. N., and KEMPTON, J. H. 1917. Breeding sweet corn resistant to the corn ear worm. *J. Agr. Research* **11**: 549-572.
- COMBS, J. B., and ZUBER, M. S. 1949. Further use of punched card equipment in predicting the performance of double-crossed corn hybrids. *Agron. J.* **41**: 485-486.
- COMSTOCK, R. E., and ROBINSON, H. F. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. *Biometrics* **4**: 254-266.
- COMSTOCK, R. E., ROBINSON, H. F., and HARVEY, P. H. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. *Agron. J.* **41**: 360-367.
- COWAN, J. R. 1943. The value of double cross hybrids involving inbreds of similar and diverse genetic origin. *Sci. Agr.* **23**: 287-296.
- CROW, J. F. 1948. Alternative hypothesis of hybrid vigor. *Genetics* **33**: 477-487.
- DARWIN, C. 1877. "The Effects of Cross and Self Fertilization in the Vegetable Kingdom," 482 pp. D. Appleton and Co., New York.
- DAVENPORT, E., and RIETZ, H. L. 1907. Type and variability in corn. *Illinois Agr. Expt. Sta. Bull.* **119**, 29.
- DAVIS, R. L. 1927. Report of the Plant Breeder. *Rept. Puerto Rico Agr. Expt. Sta.* **1927**, pp. 14-15.
- DAVIS, R. L. 1934. Maize crossing values in second-generation lines. *J. Agr. Research* **48**: 339-357.
- DICKE, F. F., and JENKINS, M. T. 1945. Susceptibility of certain strains of field corn in hybrid combinations to damage by corn earworms. *U.S. Dept. Agr. Tech. Bull.* **898**, 1-36.
- DOXTATOR, C. W., and JOHNSON, I. J. 1936. Prediction of double cross yields in corn. *J. Am. Soc. Agron.* **28**: 460-462.
- DUNN, G. M., KRAMER, H. H., and WHISTLER, R. I. 1953. Gene dosage effects on corn endosperm carbohydrates. *Agron. J.* **45**: 101-104.
- DVONCH, W., KRAMER, H. H., and WHISTLER, R. I. 1951. Polysaccharides of high amylose corn. *Cereal Chem.* **28**: 270-280.
- EAST, E. M. 1908. Inbreeding in corn. *Rept. Connecticut Agr. Expt. Sta. for 1907*, pp. 419-428.
- EAST, E. M. 1909. The distinction between development and heredity in inbreeding. *Am. Naturalist* **43**: 173-181.
- EAST, E. M. 1936. Heterosis. *Genetics* **21**: 375-397.

- ECKHARDT, R. C., and BRYAN, A. A. 1940a. Effect of method of combining the four inbred lines of a double cross of maize upon the yield and variability of the resulting double crosses. *J. Am. Soc. Agron.* **32**: 347-353.
- ECKHARDT, R. C., and BRYAN, A. A. 1940b. Effect of the method of combining two early and two late inbred lines of corn upon the yield and variability of the resulting double crosses. *J. Am. Soc. Agron.* **32**: 645-656.
- EINSET, J. 1943. Chromosome length in relation to transmission frequency of maize trisomes. *Genetics* **28**: 349-364.
- ELLIS, N. R., and ISBELL, H. S. 1926. Soft Pork Studies. II. The influence of the character of the ration upon the composition of the body fat of hogs. *J. Biol. Chem.* **69**: 219-238.
- ELLIOTT, C., and JENKINS, M. T. 1946. *Helminthosporium turcicum* leaf blight of corn. *Phytopathology* **36**: 660-666.
- FEDERER, W. T., and SPRAGUE, G. F. 1947. A comparison of variance components in corn yields trials. I. Error, tester $\times$ line and line components in top-cross experiments. *J. Am. Soc. Agron.* **39**: 453-463.
- FLINT, W. P., and HACKLEMAN, J. C. 1923. Corn varieties for chinch bug infested areas. *Illinois Agr. Expt. Sta. Bull.* **243**, 540-550.
- FLYNN, L. M., ZUBER, M. S., LEIVEKE, D. H., GRAINGER, R. B., and HOGAN, A. G. 1950. The variation in concentration of several essential amino acids and of nicotinic acid associated with increases in crude protein in corn. *Abst. Am. Chem. Soc.* 118th Meeting, p. 24C.
- FREY, K. J. 1949. Inheritance of protein and certain of its components in maize. *Agron. J.* **41**: 113-117.
- FREY, K. J. 1951. The interrelations of proteins and amino acids in corn. *Cereal Chem.* **28**: 123-132.
- FREY, K. J., BRIMHALL, B., and SPRAGUE, G. F. 1949. The effects of selection upon protein quality in the corn kernel. *Agron. J.* **41**: 399-403.
- GABELMAN, W. H. 1949. Reproduction and distribution of the cytoplasmic factor for male sterility in maize. *Proc. Nat. Acad. Sci. U.S.* **35**: 634-640.
- GARBER, R. J., and ROWLEY, H. R. 1927. A defective endosperm in the heterozygous condition as related to yield in maize. *J. Am. Soc. Agron.* **19**: 797-803.
- GARDNER, C. O., HARVEY, P. H., COMSTOCK, R. E., and ROBINSON, H. F. 1953. Dominance of genes controlling quantitative characters in maize. *Agron. J.* **45**: 186-191.
- GREEN, J. M. 1948a. Relative value of two testers for estimating top cross performance in segregating maize progenies. *J. Am. Soc. Agron.* **40**: 45-57.
- GREEN, J. M. 1948b. Inheritance of combining ability in maize hybrids. *J. Am. Soc. Agron.* **40**: 58-63.
- HARTLEY, C. P., BROWN, E. B., KYLE, C. H., and ZOOK, L. L. 1912. Cross Breeding Corn. *U.S. Dept. Agr. Bur. Plant Ind. Bull.* **218**, 1-72.
- HAYES, H. K. 1926. Present day problems of corn breeding. *J. Am. Soc. Agron.* **18**: 344-363.
- HAYES, H. K., and GARBER, R. J. 1919. Synthetic production of high protein corn in relation to breeding. *J. Am. Soc. Agron.* **11**: 309-319.
- HAYES, H. K., and JOHNSON, I. J. 1939. The breeding of improved selfed lines of corn. *J. Am. Soc. Agron.* **31**: 710-724.
- HAYES, H. K., JOHNSON, I. J., and DOXTATOR, C. W. 1931. Minnesota Corn Breeding Report. *Purnell. Corn Imp. Rept.*, p. 10.
- HAYES, H. K., JOHNSON, I. J., and STAKMAN, E. C. 1933. Reaction of maize seedlings to *Gibberella saubinetii*. *Phytopathology* **23**: 905-911.

- HAYES, H. K., MURPHY, R. P., and RINKE, E. H. 1943. A comparison of the actual yield of double crosses of maize with their predicted yield from single crosses. *J. Am. Soc. Agron.* **35**: 60-65.
- HAYES, H. K., and OLSEN, P. J. 1919. First generation crosses between standard Minnesota corn varieties. *Minn. Agr. Expt. Sta. Tech. Bull.* **183**, 5-22.
- HAYES, H. K., RINKE, E. H., and TSIANG, Y. S. 1944. The development of a synthetic variety of corn grown from inbred lines. *J. Am. Soc. Agron.* **36**: 998-1000.
- HAYES, H. K., RINKE, E. H., and TSIANG, Y. S. 1946. Experimental studies of convergent improvement and backcrossing in corn. *Minn. Agr. Expt. Sta. Tech. Bull.* **172**, 3-40.
- HIXON, R. M., and SPRAGUE, G. F. 1942. Waxy starch of maize and other cereals. *J. Ind. Eng. Chem.* **34**: 959-962.
- HOEGEMEYER, L. C. 1941. An association of root injury by white grubs, *Phyllophaga* spp. and lodging of crossbred strains of corn. *J. Am. Soc. Agron.* **33**: 1100-1107.
- HOLBERT, J. R., FLINT, W. P., BIGGER, J. H., and DUNGAN, G. H. 1935. Resistance and susceptibility of corn strains to second brood chinch bugs. *Iowa State Coll. J. Sci.* **9**: 413-426.
- HOOKE, A. L., and DICKSON, J. G. 1952. Resistance to *Pythium* manifest by excised corn embryos at low temperatures. *Agron. J.* **44**: 443-447.
- HOOVER, M. M. 1932. Inheritance studies of the reaction of selfed lines of maize to smut (*Ustilago zeae*). *West Virginia Agr. Expt. Sta. Bull.* **253**: 1-32.
- HOPKINS, C. G. 1899. Improvement in the chemical composition of the corn kernel. *Illinois Agr. Expt. Sta. Bull.* **55**, 205-240.
- HUBER, L. L., and STRINGFIELD, G. H. 1942. Aphid infestation of strains of corn as an index of their susceptibility to corn borer attack. *J. Agr. Research* **64**: 283-291.
- HULL, F. H. 1945. Recurrent selection and specific combining ability in corn. *J. Am. Soc. Agron.* **37**: 134-145.
- HULL, F. H. 1946. Overdominance and corn breeding where hybrid seed is not feasible. *J. Am. Soc. Agron.* **38**: 1100-1103.
- HULL, F. H. 1947. Cryptic homozygous lines. *J. Am. Soc. Agron.* **39**: 438-439.
- HULL, F. H. 1952. Recurrent selection and overdominance. in "Heterosis," Chapter 28, pp. 451-473. Iowa State College Press, Ames, Iowa.
- IMMER, F. R. 1927. The inheritance to reaction to *Ustilago zeae* in maize. *Minn. Agr. Expt. Sta. Tech. Bull.* **51**, 5-55.
- INGERSOLL, C. L. 1882. *Purdue University. 7th Ann. Rept.*, p. 87.
- JENKINS, M. T. 1929. Correlation studies with inbred and crossbred strains of maize. *J. Agr. Research* **39**: 677-721.
- JENKINS, M. T. 1934. Methods of estimating the performance of double crosses in corn. *J. Am. Soc. Agron.* **26**: 199-204.
- JENKINS, M. T. 1935. The effect of inbreeding and of selection within inbred lines of maize upon the hybrids made after successive generations of selfing. *Iowa State Coll. J. Sci.* **3**: 429-450.
- JENKINS, M. T. 1940. The segregation of genes affecting yield of grain in maize. *J. Am. Soc. Agron.* **32**: 55-63.
- JENKINS, M. T., and BRUNSON, A. M. 1932. Methods of testing inbred lines of maize in crossbred combinations. *J. Am. Soc. Agron.* **24**: 523-530.
- JENKINS, M. T., and ROBERT, A. I. 1952. Inheritance of resistance to the leaf blight of corn caused by *Helminthosporium turcicum*. *Agron. J.* **44**: 136-140.
- JENKINS, M. T., ROBERT, A. I., and FINDLEY, W. R., JR. 1952. Inheritance of resistance of *Helminthosporium turcicum* leaf blight in populations of F₃ progenies. *Agron. J.* **44**: 438-442.

- JENKINS, M. T., ROBERT, A. I., and FINDLEY, W. R., JR. 1954. Recurrent selection as a method for concentrating genes for resistance to *Helminthosporium turcicum* leaf blight in corn. *Agron. J.* **46**: 89-94.
- JOHNSON, I. J., and HAYES, H. K. 1936. The combining ability of inbred lines of Golden Bantam sweet corn. *J. Am. Soc. Agron.* **28**: 246-252.
- JOHNSON, I. J., and HAYES, H. K. 1940. The value in hybrid combinations of inbred lines of corn selected from single crosses by the pedigree method of breeding. *J. Am. Soc. Agron.* **32**: 479-485.
- JONES, D. F. 1918. The effects of inbreeding and crossbreeding upon development. *Connecticut Agr. Expt. Sta. Bull.* **207**, 5-100.
- JONES, D. F. 1922. The productiveness of single and double cross first generation hybrids. *J. Am. Soc. Agron.* **14**: 241-252.
- JONES, D. F. 1939. Continued inbreeding in maize. *Genetics* **24**: 462-473.
- JONES, D. F. 1945. Heterosis resulting from degenerative changes. *Genetics* **30**: 527-542.
- JONES, D. F. 1950. The interrelation of plasmagenes and chromogenes in pollen production in maize. *Genetics* **35**: 507-512.
- JONES, D. F. 1951. The cytoplasmic separation of species. *Proc. Natl. Acad. Sci. U.S.* **37**: 408-410.
- JONES, D. F. 1952. Plasmagenes and chromogenes in heterosis. in "Heterosis," Chapter 14, pp. 224-235. Iowa State College Press, Ames, Iowa.
- JONES, D. F., and EVERETT, H. L. 1949. Hybrid field corn. *Connecticut Agr. Expt. Sta. Bull.* **532**, 3-39.
- JONES, D. F., and MANGELSDORF, P. J. 1951. The production of hybrid corn seed without detasseling. *Connecticut Agr. Expt. Sta. Bull.* **550**, 5-21.
- JONES, D. F., and SINGLETON, W. R. 1934. Crossed sweet corn. *Connecticut Agr. Expt. Sta. Bull.* **361**, 489-536.
- JORGENSEN, L., and BREWBAKER, H. E. 1927. A comparison of selfed lines of corn and first generation crosses between them. *J. Am. Soc. Agron.* **19**: 819-830.
- JOSEPHSON, L. M., and JENKINS, M. T. 1948. Male sterility in corn hybrids. *J. Am. Soc. Agron.* **40**: 267-274.
- KELLER, K. R. 1949. A comparison involving the number of and relationship between testers in evaluating inbred lines of maize. *Agron. J.* **41**: 323-331.
- KIESSELBACH, T. A. 1922. Corn investigations. *Nebraska Agr. Expt. Sta. Research Bull.* **20**, 5-151.
- KIESSELBACH, T. A. 1930. The use of advanced generation hybrids as parents of double cross seed corn. *J. Am. Soc. Agron.* **22**: 614-626.
- KIESSELBACH, T. A. 1933. The possibilities of modern corn breeding. *Proc. World Grain Exhib. and Conf., Canada* **2**: 92-112.
- KINMAN, M. L., and SPRAGUE, G. F. 1945. Relation between number of parental lines and theoretical performance of synthetic varieties of corn. *J. Am. Soc. Agron.* **37**: 341-351.
- KRAMER, H. H., and WHISTLER, R. I. 1949. Quantitative effects of certain genes on the amylose content of corn endosperm. *J. Am. Soc. Agron.* **41**: 409-411.
- KYLE, C. H. 1918. Shuck protection for ear corn. *U.S. Dept. Agr. Bull.* **708**, 1-16.
- LINDSTROM, E. W. 1931. Prepotency of inbred sires on commercial varieties of maize. *J. Am. Soc. Agron.* **23**: 652-661.
- LINDSTROM, E. W. 1939. Analysis of modern maize breeding principles and method. *Proc. 7th Intern. Genet. Congr. Edinburgh, Scot. 1939*, pp. 191-196.
- LIVINGSTON, J. E. 1951. Effect of low temperature on the germination of artificially dried seed corn. *Nebraska Agr. Expt. Sta. Research Bull.* **169**, 3-14.

- LONNQUIST, J. H. 1949. The development and performance of synthetic varieties of corn. *Agron. J.* **41**: 153-156.
- LONNQUIST, J. H. 1950. The effect of selection for combining ability within segregating lines of corn. *Agron. J.* **42**: 503-508.
- LONNQUIST, J. H. 1951. Recurrent selection as a means of modifying combining ability in corn. *Agron. J.* **43**: 311-315.
- LORAIN, J. 1825. "Nature and Reason Harmonized in the Practice of Husbandry," 563 pp. Carey and Lea, Philadelphia.
- MANGELSDORF, P. C. 1928. The effects of a lethal on the heterozygote in maize. *J. Heredity* **19**: 123-131.
- MATHER, K. 1942. The balance of polygenic combinations. *J. Genet.* **43**: 309-336.
- MATZINGER, D. F. 1953. Comparison of three types of testers for the evaluation of inbred lines of corn. *Agron. J.* **45**: 493-495.
- MCCOLLOCH, J. W. 1921. The corn leaf aphid (*Aphis Maidis Fitch*) in Kansas. *J. Econ. Entomol.* **14**: 89-94.
- MCINDOE, K. G. 1931. The inheritance of the reaction of maize to *Gibberella saubinetii*. *Phytopathology* **21**: 615-639.
- MEYERS, M. T., HUBER, L. L., NEISWANDER, C. R., RICHEY, F. D., and STRINGFIELD, G. H. 1937. Experiments on breeding corn resistant to the European corn borer. *U.S. Dept. Agr. Tech. Bull.* **583**, 1-29.
- MILLANG, A., and SPRAGUE, G. F. 1940. The use of punched card equipment in predicting the performance of corn double crosses. *J. Am. Soc. Agron.* **32**: 815-816.
- MILLER, P. A., and BRIMHALL, B. 1951. Factors influencing the oil and protein content of the corn kernel. *Agron. J.* **43**: 305-311.
- MILLER, P. A., HURST, T. L., and BRIMHALL, B. 1952. Relationships of lysine and niacin with the crude protein and certain protein components in corn grain. *Agron. J.* **44**: 343-345.
- MILLER, R. C., AURAND, L. W., and FLACK, W. R. 1950. Amino acids in high and low protein corn. *Science* **112**: 57-58.
- MITCHELL, H. H., and BEADLES, J. R. 1944. Corn germ a valuable protein food. *Science* **99**: 129-130.
- MORGAN, W. L. 1940. Pasting and identification of starches. *Ind. Eng. Chem. (Anal. Ed.)* **12**: 313-317.
- MORROW, G. E., and GARDNER, F. D. 1893. Field experiments with corn, 1892. *Illinois Agr. Expt. Sta. Bull.* **25**, 173-203.
- MURPHY, R. P. 1942. Convergent improvement with four inbred lines of corn. *J. Am. Soc. Agron.* **34**: 138-150.
- NEAL, N. P. 1935. The decrease in yielding capacity in advanced generations of hybrid corn. *J. Am. Soc. Agron.* **27**: 666-670.
- NILSSON-LEISSNER, G. 1927. Relation of selfed strains of corn to F_1 crosses between them. *J. Am. Soc. Agron.* **19**: 440-454.
- PAINTER, R. H., and BRUNSON, A. M. 1940. Differential injury within varieties, inbred lines and hybrids of field corn caused by the corn earworm *Heliothis armigera* (HBN). *J. Agr. Research* **61**: 81-100.
- PANSE, V. G. 1940. The application of genetics to plant breeding. II. The inheritance of quantitative characters and plant breeding. *J. Genet.* **40**: 283-302.
- PATCH, L. H. 1943. Survival, weight and location of European corn borers feeding on resistant and susceptible field corn. *J. Agr. Research* **66**: 7-19.
- PATCH, L. H., and EVERLY, R. T. 1945. Resistance of dent corn inbred lines to survival of first-generation European corn borer larvae. *U.S. Dept. Agr. Tech. Bull.* **893**, 1-10.

- PAYNE, K. T., and HAYES, H. K. 1949. A comparison of combining ability in F_1 and F_2 lines of corn. *Agron. J.* **41**: 383-388.
- PHILLIPS, W. J., and BARBER, G. W. 1931. The value of husk protection to corn ears in limiting corn ear worm injury. *Virginia Agr. Expt. Sta. Tech. Bull.* **43**, 3-24.
- PINNELL, E. L. 1943. The variability of certain quantitative characters of a double cross hybrid in corn as related to the method of combining the four inbreds. *J. Am. Soc. Agron.* **35**: 508-514.
- PINNELL, E. L. 1949. Genetic and environmental factors affecting seed corn germination at low temperatures. *Agron. J.* **41**: 562-568.
- PINNELL, E. L., RINKE, E. H., and HAYES, H. K. 1952. Gamete selection for specific combining ability. in "Heterosis," Chapter 24, pp. 378-388. Iowa State College Press, Ames, Iowa.
- RANDOLPH, L. F. 1942. The influence of heterozygosis on fertility and vigor in autotetraploid maize. *Genetics* **27**: 163.
- RHOADES, M. M. 1931. Cytoplasmic inheritance of male sterility in *Zea Mays*. *Science* **73**: 340-341.
- RHOADES, M. M. 1933. The cytoplasmic inheritance of male sterility in *Zea Mays*. *J. Genet.* **27**: 71-93.
- RHOADES, M. M. 1943. Genic induction of an inherited cytoplasmic difference. *Proc. Nat. Acad. Sci. U.S.* **29**: 327-329.
- RHOADES, M. M. 1950. Gene induced mutation of a heritable cytoplasmic factor producing male sterility in maize. *Proc. Natl. Acad. Sci. U.S.* **36**: 634-635.
- RHOADES, V. H. 1935. The location of a gene for disease resistance in maize. *Proc. Natl. Acad. Sci. U.S.* **21**: 243-246.
- RICHEY, F. D. 1922. The experimental basis for the present status of corn breeding. *J. Am. Soc. Agron.* **14**: 1-17.
- RICHEY, F. D. 1924. Effects of selection on the yield of a cross between varieties of corn. *U.S. Dept. Agr. Bull.* **1209**, 1-19.
- RICHEY, F. D. 1927. The convergent improvement of selfed lines of corn. *Am. Naturalist* **61**: 430-449.
- RICHEY, F. D. 1944. Maize hybrids susceptible to ear worm. *J. Heredity* **35**: 327-328.
- RICHEY, F. D. 1945. Isolating better foundation inbreds for use in corn hybrids. *Genetics* **30**: 455-471.
- RICHEY, F. D. 1947. Corn breeding, gamete selection, the *Oenothera* method and related miscellany. *J. Am. Soc. Agron.* **39**: 403-412.
- RICHEY, F. D., and DAWSON, R. F. 1948. A survey of the possibilities and methods of breeding high niacin corn (Maize). *Plant Physiol.* **23**: 238-254.
- RICHEY, F. D., and DAWSON, R. F. 1951. Experiments on the inheritance of niacin in corn (Maize). *Plant Physiol.* **26**: 475-493.
- RICHEY, F. D., and MAYER, L. S. 1925. The productiveness of successive generations of self-fertilized lines of corn and of crosses between them. *U.S. Dept. Agr. Bull.* **1354**, 1-18.
- RICHEY, F. D., and SPRAGUE, G. F. 1931. Experiments on hybrid vigor and convergent improvement in corn. *U.S. Dept. Agr. Tech. Bull.* **267**, 22.
- RICHEY, F. D., STRINGFIELD, G. H., and SPRAGUE, G. F. 1934. The loss in yield that may be expected from planting second generation double cross seed corn. *J. Am. Soc. Agron.* **26**: 196-199.
- ROBINSON, H. F., COMSTOCK, R. E., and HARVEY, P. H. 1949. Estimates of heritability and degree of dominance in corn. *Agron. J.* **41**: 353-399.
- ROBINSON, H. F., COMSTOCK, R. E., and HARVEY, P. H. 1951. Genetic and phenotypic correlations in corn and their implications in selection. *Agron. J.* **43**: 282-287.

- RODRIGUEZ, I. D., HUNT, C. H., and BETHKE, R. M. 1950. The protein, niacin and pantothenic acid contents of corn inbred lines. *Cereal Chem.* **27**: 67-70.
- ROGERS, J. S., and EDWARDSON, J. R. 1952. The utilization of cytoplasmic male-sterile inbreds in the production of corn hybrids. *Agron. J.* **44**: 8-13.
- ROJAS, B. A. 1951. Analysis of a group of experiments on combining ability in corn. M.S. Thesis, Iowa State College, Ames, Iowa.
- ROJAS, B. A., and SPRAGUE, G. F. 1952. A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with location and years. *Agron. J.* **44**: 462-466.
- ROMAN, H., and ULLSTRUP, A. J. 1951. The use of A-B translocations to locate genes in maize. *Agron. J.* **43**: 450-454.
- RUSH, G. E., and NEAL, N. P. 1951. The effect of maturity and other factors on stands of corn at low temperatures. *Agron. J.* **43**: 112-116.
- SABOE, L. C., and HAYES, H. K. 1941. Genetic studies of reactions to smut and firing in maize by means of chromosomal translocations. *J. Am. Soc. Agron.* **33**: 463-470.
- SCHNEIDER, E. O., EARLEY, E. B., and DETURK, E. E. 1952. Nitrogen fractions of the component parts of the corn kernel as affected by selection and soil nitrogen. *Agron. J.* **44**: 161-169.
- SCHWARTZ, D. 1951a. A case of male sterility in maize involving gene-cytoplasm interaction. *Records Genetics Soc. Amer.* **30**: 123.
- SCHWARTZ, D. 1951b. The interaction of nuclear and cytoplasmic factors in the inheritance of male sterility in maize. *Genetics* **36**: 676-696.
- SHAMEL, A. D. 1905. The effect of inbreeding in plants. *Yearbook Agr. U.S. Dept. Agr.*, pp. 377-392.
- SHULL, G. H. 1908. The composition of a field of maize. *Am. Breed. Assoc. Rept.* **4**: 296-301.
- SHULL, G. H. 1909. A pure line method of corn breeding. *Am. Breed. Assoc. Rept.* **5**: 51-59.
- SINGLETON, W. R. 1943. Breeding behavior of C₃₀, a diminutive P₃₉ mutant whose hybrids show increased vigor. *Genetics* **28**: 89.
- SINGLETON, W. R., and NELSON, O. E. 1945. The improvement of naturally cross-pollinated plants by selection in self-fertilized lines. IV. Combining ability of successive generations of inbred sweet corn. *Connecticut Agr. Expt. Sta. Bull.* **490**, 458-498.
- SMITH, A. L., HOPPE, P. E., and HOLBERT, J. R. 1938. Development of a differential inoculation technic for *Diplodia* stalk rot of corn. *Phytopathology* **28**: 497-504.
- SMITH, F. L., and MADSEN, C. B. 1949. Susceptibility of inbred lines of corn to *Fusarium* ear rot. *Agron. J.* **41**: 347-348.
- SMITH, L. H. 1909. The effect of selection upon certain physical characters of the corn plant. *Illinois Agr. Expt. Sta. Bull.* **132**.
- SMITH, L. H., and BRUNSON, A. M. 1925. An experiment in selecting corn for yield by the method of the ear-row breeding plot. *Illinois Agr. Expt. Sta. Bull.* **271**, 566-583.
- SMITH, L. H., and BRUNSON, A. M. 1928. Experiments in crossing varieties as a means of improving productiveness in corn. *Illinois Agr. Expt. Sta. Bull.* **306**, 374-386.
- SNELLING, R. O., BLANCHARD, R. A., and BIGGER, J. H. 1940. Resistance of corn strains to the leaf aphid. *J. Am. Soc. Agron.* **32**: 371-381.
- SNELLING, R. O., and DAHMS, R. G. 1937. Resistant varieties of sorghum and corn in relation to chinch bug control in Oklahoma. *Oklahoma Agr. Expt. Sta. Bull.* **232**, 3-22.

- SPRAGUE, G. F. 1939. An estimation of the number of top-crossed plants required for adequate representation of a corn variety. *J. Am. Soc. Agron.* **31**: 11-16.
- SPRAGUE, G. F. 1942. Production of hybrid corn. *Iowa Agr. Expt. Sta. Bull.* **556**, 1-48.
- SPRAGUE, G. F. 1946. Early testing of inbred lines of corn. *J. Am. Soc. Agron.* **38**: 108-117.
- SPRAGUE, G. F. 1952. Early testing and recurrent selection. in "Heterosis," Chapter 26, pp. 400-417. Iowa State College Press, Ames, Iowa.
- SPRAGUE, G. F., and BRIMHALL, B. 1949. Quantitative inheritance of oil in the corn kernel. *Agron. J.* **41**: 30-33.
- SPRAGUE, G. F., and BRIMHALL, B. 1950. Relative effectiveness of two systems of selection for oil content of the corn kernel. *Agron. J.* **42**: 83-88.
- SPRAGUE, G. F., BRIMHALL, B., and HIXON, R. M. 1943. Some effects of the waxy gene in corn on properties of the endosperm starch. *J. Am. Soc. Agron.* **35**: 817-822.
- SPRAGUE, G. F., and FEDERER, W. T. 1951. A comparison of variance components in corn yield trials. II. Error, year $\times$ variety, location $\times$ variety and variety components. *Agron. J.* **43**: 535-541.
- SPRAGUE, G. F., and JENKINS, M. T. 1943. A comparison of synthetic varieties, multiple crosses and double crosses in corn. *J. Am. Soc. Agron.* **35**: 137-147.
- SPRAGUE, G. F., and JENKINS, M. T. 1948. The development of waxy corn for industrial use. *Iowa State College J. Sci.* **22**: 205-213.
- SPRAGUE, G. F., and MILLER, P. A. 1950. A suggestion for evaluating current concepts of the genetic mechanism of heterosis in corn. *Agron. J.* **42**: 161-162.
- SPRAGUE, G. F., and MILLER, P. A. 1952. The influence of visual selection during inbreeding on combining ability in corn. *Agron. J.* **44**: 258-262.
- SPRAGUE, G. F., MILLER, P. A., and BRIMHALL, B. 1952. Additional studies of the relative effectiveness of two systems of selection for oil content of the corn kernel. *Agron. J.* **44**: 329-331.
- SPRAGUE, G. F., and TATUM, L. A. 1942. General vs specific combining ability in single crosses of corn. *J. Am. Soc. Agron.* **34**: 923-932.
- STADLER, L. J. 1944. Gamete selection in corn breeding. *J. Am. Soc. Agron.* **36**: 988-989.
- STAKMAN, E. C., CHRISTENSEN, J. J., and BREWBAKER, H. E. 1928. Physiologic specialization in *Puccinia sorghi*. *Phytopathology* **18**: 345-354.
- STRINGFIELD, G. H. 1950. Heterozygosis and hybrid vigor in maize. *Agron. J.* **42**: 145-152.
- "Student." 1934. A calculation of the minimum number of genes in Winter's selection experiment. *Ann. Eug.* **6**: 77-82.
- TATUM, L. A. 1942. The effect of genetic constitution and processing methods on the ability of maize seed to germinate in cold soil. Ph D. thesis, Iowa State College, Ames, Iowa.
- TEAS, H. J., CAMERON, J. W., and NEWTON, A. C. 1952. Tryptophan, niacin, indole-acetic acid and carbohydrates in developing sugary and starchy maize kernels. *Agron. J.* **44**: 434-438.
- TEAS, H. J., and NEWTON, A. C. 1951. Tryptophan, niacin and indole-acetic acid in several endosperm mutants and standard line of maize. *Plant Physiol.* **26**: 494-501.
- THOMPSON, D. L. 1954. Combining ability of homozygous diploids of corn relative to lines derived by inbreeding. *Agron. J.* **46**: 133-136.
- ULLSTRUP, A. J. 1944. Further studies on a species of *Helminthosporium* parasitizing corn. *Phytopathology* **34**: 214-222.
- ULLSTRUP, A., and BRUNSON, A. M. 1947. Linkage relationships of a gene in corn determining susceptibility to a *Helminthosporium* leaf spot. *J. Am. Soc. Agron.* **39**: 606-609.

- WALTER, E. V., and BRUNSON, A. M. 1940. Differential susceptibility of corn hybrids to *Aphis maidis*. *J. Econ. Entomol.* **33**: 623-628.
- WALTER, E. V., and BRUNSON, A. M. 1946. Selection for aphid resistance within inbred lines of maize. *J. Am. Soc. Agron.* **38**: 974-977.
- WELLHAUSEN, E. J. 1937. Genetics of resistance to bacterial wilt in maize. *Iowa Agr. Expt. Sta. Research Bull.* **244**, 73.
- WELLHAUSEN, E. J. 1952. Heterosis in a new population. in "Heterosis," Chapter 27, pp. 418-450. Iowa State College Press, Ames, Iowa.
- WELLHAUSEN, E. J., ROBERTS, L. M., and HERNANDEZ, X. E. 1952. Races of maize in Mexico. Bussey Inst. of Harvard Univ., pp. 9-223.
- WENTZ, J. B., and GOODSSELL, S. F. 1929. Recessive defects and yield in corn. *J. Agr. Research* **38**: 505-510.
- WILLIAMS, C. G., and WELTON, F. A. 1915. Corn experiments. *Ohio Agr. Expt. Sta. Bull.* **282**, 69-109.
- WINTER, F. L. 1929. The mean and variability as affected by continuous selection for composition in corn. *J. Agr. Research* **39**: 451-476.
- WOODWORTH, C. M. 1931. Illinois corn breeding report. *Purnell Corn Imp. Rept.*, pp. 48-49.
- WOODWORTH, C. M., LENG, E. R., and JUGENHEIMER, R. W. 1952. Fifty generations of selection for protein and oil in corn. *Agron. J.* **44**: 60-65.
- WORTMAN, L. S., and RINKE, E. H. 1951. Seed corn injury at various stages of processing and its effect upon cold test performance. *Agron. J.* **43**: 299-305.
- WRIGHT, S. 1922. The effects of inbreeding and cross breeding on guinea-pigs. III. Crosses between highly inbred families. *U.S. Dept. Agr. Tech. Bull.* **1121**, 1-61.
- WU, S. K. 1939. The relationship between the origin of selfed lines of corn and their value in hybrid combinations. *J. Am. Soc. Agron.* **31**: 131-140.
- YATES, F. 1940. Modern experimental design and its function in plant selection. *Empire J. Expt. Agr.* **8**: 223-230.
- YERMANOS, D. M. 1952. Comparative efficiency of three methods of isolating inbred lines of corn. M.S. thesis, Iowa State College, Ames, Iowa.

CHAPTER VI

Mineral Nutrition of Corn

J. D. SAYRE

I. Introduction

The mineral nutrition of corn is a very broad subject. It has been studied for many years. This chapter reports some of the more recent work and summarizes some of the results obtained from studies of inbred lines and hybrids. There are a number of chemical elements which are concerned with the mineral nutrition of corn. They may be divided into three main groups: first, a group of six major elements, second, a group of six minor elements, and third, a group of twelve or more accessory elements often found in corn. Nitrogen, phosphorus, sulfur, potassium, calcium, and magnesium are the six major elements and usually occur in greatest amounts. The six minor elements are iron, manganese, boron, copper, zinc, and molybdenum. Although only small amounts of these elements are required, they are essential for normal plant growth. These twelve elements are required by most green plants.

In addition to the twelve elements necessary for the proper development of corn, many others which are classed as accessory elements are often found in corn tissue. These elements are silicon, aluminum, nickel, cobalt, chromium, tin, lead, silver, barium, strontium, chlorine, and sodium. Some of these may have some function in the physiology of the plant. Others may have some effect in replacing certain essential elements, whereas others are toxic in high quantity.

As the textbook on physiology by Meyer and Anderson (1952) discusses thoroughly the function of all these elements in the growth of plants, including corn, the subject will not be discussed here. The main emphasis in this chapter is given to mineral accumulation in the corn plant and its relation to corn growth and development. The differential accumulation of elements by inbred lines and hybrids is discussed, and some recent results on mineral accumulation in margins of the leaves are reported.

A large number of plant samples have been collected at various stages through the season for measurement and chemical analysis of the different plant parts at different stages of development. This article

will attempt to summarize some of the results of these experiments by Sayre and Morris (1938, 1939), by Sayre, Gammon, and Converse (1940), and by Sayre (1946, 1947a).

II. Growth and Development of the Corn Plant

Mineral accumulation in corn was investigated by careful analyses of the dried samples of corn tissue harvested every few days throughout the growing season. A large number of samples representing different tissues as they had developed during the season were available. The frequent sampling and the sample size needed for adequate representation required the growing of a large number of plants. Uniform soils aid materially in obtaining comparable samples.

After the young plants emerge from the soil they show only a few leaves until growth is well under way. At the knee-high stages leaves are still unrolling from the growing point of the plant, which is only a few inches high. Plants taken at such early stages consist largely of leaves, since other structures are then just developing.

Growth is very rapid after the knee-high stage, which at Wooster usually occurs about the first of July. By the end of the month tissue differentiation of the vegetative portion of the plant is largely completed. At this latter state the plant may be 6, 7, or more feet tall, and consists of leaves, stem, tassel, and a small ear.

Seeds begin to form after pollination and fertilization, and synthesized carbohydrates and minerals from the soil move into the grain very rapidly until about the last of August, when the grain is fairly well along toward maturity. At Wooster not much growth occurs after the month of August, but the process of maturing and ripening of the grain goes on. Some time before this the lower leaves and some other tissues have begun to disintegrate, and the tassel dries up. At maturity, which usually occurs about the time of frost in this locality, most of the dry matter has been laid down in the ear and the process from then on is merely one of losing water or drying out of the grain along with the dying, drying out, and disintegration of the rest of the plant.

III. Percentage Composition of the Tissues

The percentage composition of the tissues is determined by chemical or spectrographic analysis. Table I gives an estimation of the percentage composition of the different tissues of the corn plant just before maturity, after growth had ceased but before disintegration of the tissues had occurred. These values were obtained from analyses of corn plants over a considerable period of time. They represent the average

composition of the tissues of the plant as far as the different elements are concerned.

An examination of these data shows that the corn plant does not have a very high concentration of any of the mineral elements. The principal material in the corn plant is starch which is stored in the grain.

The three major parts of the corn plant are leaves, stem, and ear, and Table I shows the proportion of dry matter in each. The roots are

TABLE I

ESTIMATED PERCENTAGE COMPOSITION OF TISSUES OF THE CORN PLANT JUST BEFORE MATURITY

	<i>Dry matter,</i> %	<i>Nitrogen,</i> %	<i>Phosphorus,</i> %	<i>Potassium,</i> %	<i>Calcium,</i> %	<i>Magnesium,</i> %
Leaves ^a	12	2.0	0.25	1.6	0.3	0.25
Sheath	6	0.4	0.10	1.2	0.3	0.20
Stem ^b	22	0.7	0.11	1.2	0.1	0.09
Tassel	1	0.7 ^c	0.10	1.0	0.1	0.08
Ear						
Grain	45	1.5	0.29	0.35	0.01	0.08
Cob	8	0.2	0.12	0.40	0.09	0.06
Husks	5	0.4	0.11	1.10	0.09	0.07
Shank	1	0.5	0.12	1.10	0.09	0.07

^a 78 per cent of the leaf tissue was blade (blade margin = 12 per cent) and 22 per cent was midrib.

^b 75 per cent of the stem tissue consisted of internodes and 25 per cent of nodes.

^c 2.4 per cent before pollen shed.

not included in this estimation, but other studies have shown that an average corn plant has about 30 g. of roots. The percentage composition of the five major elements shown in this table are estimates of the average composition of the tissue. The composition would be different for corn plants grown under greatly different fertilizer treatments. Inbred lines and hybrids vary considerably in their percentage composition even when grown on similar soil. This table, therefore, presents only an approximation of the average composition of the different tissues of the corn plant.

The major parts of the corn plant can be subdivided into many other tissues which differ from each other. The stalk or stem has from 12 to 16 nodes, internodes, and leaves. These could be analyzed separately; thus a complete dissection of the corn plant would result in a large number of samples. Such fine dissections of the corn plant are not usually made, but many investigators have divided the plant into upper, middle, and lower parts. The middle section usually includes the ear node and leaf and the node above and below the ear node. When

TABLE II

DRY WEIGHT OF LEAVES PER PLANT AND THE PERCENTAGE COMPOSITION OF MINERAL ELEMENTS. OHIO K35, 1940

<i>Date</i>	<i>Dry weight, g.</i>	<i>Nitrogen, %</i>	<i>Phosphorus, %</i>	<i>Potassium, %</i>	<i>Calcium, %</i>	<i>Magnesium, %</i>
June 20	5	3.0	0.26	4.2	0.44	0.16
23	8	2.8	0.28	4.4	0.38	0.19
26	9	3.1	0.31	4.3	0.40	0.18
29	11	3.2	0.31	3.9	0.45	0.18
July 2	14	3.1	0.31	3.6	0.49	0.17
5	18	3.1	0.32	3.3	0.50	0.16
8	23	3.3	0.32	3.2	0.48	0.16
11	29	3.0	0.33	3.0	0.43	0.16
14	35	3.0	0.33	3.0	0.37	0.17
17	41	3.0	0.34	2.9	0.32	0.18
20	46	3.0	0.35	2.8	0.29	0.18
23	51	2.9	0.35	2.7	0.29	0.19
26	55	2.9	0.35	2.5	0.30	0.20
29	59	2.9	0.34	2.3	0.32	0.22
Aug. 1	62	2.9	0.34	2.1	0.33	0.23
4	63	2.9	0.33	2.1	0.33	0.25
7	61	2.9	0.33	2.1	0.32	0.26
10	59	2.8	0.33	2.1	0.32	0.26
13	58	2.8	0.33	2.1	0.33	0.26
16	60	2.7	0.32	2.1	0.33	0.26
19	62	2.7	0.31	2.0	0.35	0.25
22	65	2.6	0.31	1.9	0.35	0.25
25	66	2.6	0.30	1.8	0.35	0.24
28	65	2.6	0.30	1.7	0.37	0.24
31	63	2.5	0.30	1.6	0.38	0.25
Sept. 3	62	2.4	0.29	1.6	0.38	0.25
6	61	2.1	0.28	1.6	0.38	0.24
9	61	2.1	0.27	1.6	0.37	0.24
12	61	2.0	0.25	1.6	0.36	0.24
15	61	2.0	0.25	1.7	0.35	0.24
18	61	1.9	0.24	1.7	0.30	0.24

studies are made of such fine dissections of the corn plant, there is usually a rather gradual change from one plant part to another in chemical composition.

The production of dry matter and the mineral accumulation in Ohio K35 was studied at Wooster in 1940 in great detail. Data from this experiment are reported in Tables II, III, and IV. The dry weights of the leaves at the different sampling dates and the percentages of nitrogen,

TABLE III

DRY WEIGHT OF STEM TISSUE AND ACCUMULATION OF MINERAL ELEMENTS IN GRAMS
PER PLANT. OHIO K35, IN 1940

<i>Date</i>	<i>Dry weight, g.</i>	<i>Nitrogen, g.</i>	<i>Phosphorus, g.</i>	<i>Potassium, g.</i>	<i>Calcium, g.</i>	<i>Magnesium, g.</i>
June 29	8	0.20	0.023	0.22	0.039	0.020
July 2	10	0.28	0.029	0.52	0.043	0.022
5	15	0.37	0.044	0.77	0.053	0.030
8	24	0.48	0.065	1.04	0.063	0.048
11	34	0.62	0.089	1.30	0.077	0.073
14	48	0.77	0.118	1.55	0.096	0.104
17	63	0.93	0.153	1.81	0.120	0.137
20	81	1.13	0.195	2.06	0.142	0.164
23	99	1.33	0.242	2.36	0.158	0.186
26	117	1.52	0.285	2.59	0.169	0.207
29	130	1.61	0.311	2.68	0.177	0.228
Aug. 1	130	1.61	0.317	2.64	0.188	0.242
4	137	1.51	0.312	2.50	0.198	0.244
7	137	1.44	0.314	2.39	0.207	0.237
10	139	1.41	0.324	2.34	0.216	0.226
13	143	1.41	0.334	2.34	0.220	0.213
16	145	1.41	0.334	2.34	0.215	0.201
19	145	1.41	0.324	2.36	0.195	0.192
22	145	1.44	0.314	2.36	0.169	0.192
25	146	1.45	0.307	2.36	0.140	0.199
28	147	1.42	0.308	2.26	0.137	0.207
31	147	1.30	0.308	2.11	0.134	0.208
Sept. 3	144	1.19	0.302	1.94	0.135	0.202
6	143	1.08	0.282	1.80	0.138	0.191
9	141	1.01	0.261	1.71	0.150	0.182
12	140	0.96	0.243	1.63	0.158	0.175
15	143	0.93	0.228	1.57	0.163	0.173
18	144	0.90	0.218	1.63	0.141	0.170

phosphorus, potassium, calcium, and magnesium in the dry matter of the leaves are reported in Table II. Sulfur was not determined in these samples.

The data on potassium are the most interesting because they show a gradual decrease from a very high percentage in the leaf tissue at the beginning of the summer to a rather low value at the end of the season. Nitrogen content decreases throughout the season, and phosphorus content tends to reach a maximum about the middle of the season and then to decrease as the plant matures. Calcium percentage decreases throughout the season, and the magnesium content of the leaves

shows a rather definite rise in percentage composition up until the latter part of the season, when there is a slight decrease.

Studies of the percentage composition of the different tissues of the corn plant are valuable in showing what is happening as the different tissues develop during the season. But a knowledge of the dry weight of the tissue is essential in order to interpret the accumulation and movement of the different elements. The data in Table III show the accumulation of mineral elements in the stem tissue of the corn plant. The table shows the dry weight of the stems (including sheath tissue) as they developed throughout the season and the grams of the different elements calculated from the percentage composition and total weight of the tissue. Such calculations were made on all tissues of the corn plant and the total quantity of mineral elements in each tissue determined.

Table III shows that nitrogen increases in the stem until about the middle of the season and then decreases. This means that as the stem is growing there is an accumulation of nitrogen, but that after the plant has reached the maximum size there is a movement of nitrogen out of the stem into the other tissue. A similar statement can be made concerning the other elements listed in Table III.

The accumulation and movement of mineral elements can be determined by calculating the total amount in each tissue at the different stages of development. The sum of the elements from the individual parts of the plant gives the total amount accumulated by plant. When the whole plant is used as a unit, it is impossible to study the movement of material from one tissue to another. It is also very difficult to sample a whole corn plant because of differences in the amount and texture of the tissues which compose it. Many successful experiments have been carried out where the stover or fodder (leaves, sheath, stem, husks, and shank) has been separated from the grain (Jones and Huston, 1914; Hopper, 1925; and Miller, 1943), and valuable results obtained from such studies.

IV. Accumulation by the Whole Plant

The accumulation of elements by the whole plant has been reported in detail by Sayre (1947b), but only portions of the data can be shown here. Dry matter and mineral accumulation taken in grams per plant have been converted to pounds per acre, and the values of dry matter and five elements are shown in Table IV.

The acre of corn accumulated about 6 tons of dry matter and 144 pounds of nitrogen during the growing season. A careful examination of the data shows that there was a slight decrease between some of the

TABLE IV

TOTAL ACCUMULATION OF DRY MATTER AND MINERAL ELEMENTS IN CORN IN POUNDS PER ACRE. OHIO K35, IN 1940

<i>Date</i>	<i>Dry weight, lb.</i>	<i>Nitrogen, lb.</i>	<i>Phosphorus, lb.</i>	<i>Potassium, lb.</i>	<i>Calcium, lb.</i>	<i>Magnesium, lb.</i>
June 20	118	3.5	0.3	4.9	0.5	0.2
23	188	5.2	0.5	8.2	0.7	0.4
26	212	6.6	0.7	9.2	1.3	0.6
29	447	13.0	1.3	15.3	2.1	0.9
July 2	565	16.7	1.7	24.0	2.6	1.1
5	777	21.9	2.4	32.3	3.4	1.4
8	1107	27.8	3.3	41.7	4.1	2.0
11	1484	35.1	4.3	51.3	4.8	2.8
14	1955	42.6	5.5	61.0	5.3	3.8
17	2449	50.9	6.9	70.9	5.9	5.0
20	2991	58.6	8.3	79.8	6.5	5.9
23	3533	66.6	9.9	87.6	7.2	6.6
26	4051	73.7	11.2	92.8	7.9	7.4
29	4734	83.6	13.5	99.4	8.8	8.8
Aug. 1	5581	95.8	15.3	105.3	9.7	10.0
4	6147	98.0	16.9	108.6	10.0	10.6
7	6570	99.1	17.5	110.9	10.3	10.7
10	7183	107.2	18.6	112.8	10.8	11.1
13	7701	115.9	20.7	113.5	11.8	11.2
16	8313	120.8	21.5	113.0	12.1	11.3
19	8714	126.2	22.4	113.5	11.8	11.1
22	9137	132.8	22.8	113.7	11.3	11.2
25	9608	138.9	23.8	113.7	10.8	11.5
28	10032	142.2	25.2	110.7	10.6	11.7
31	10409	141.8	26.5	106.2	10.6	11.9
Sept. 3	10715	140.8	27.6	102.2	10.6	11.9
6	11099	139.7	28.1	99.9	10.6	11.8
9	11445	139.9	28.5	98.4	10.7	11.9
12	11846	141.1	29.2	98.0	10.8	11.9
15	12199	142.7	30.0	98.2	10.9	12.1
18	12387	144.1	30.2	98.4	10.7	12.3

sampling days, indicating a slight loss of some of these elements. This may be caused by a leaching or slight loss of tissue due to shattering or disintegration or may be due to errors in sampling. A decrease in total nitrogen is indicated in the samples taken about September 3. A different set of plants was taken on each sampling date; thus the errors of sampling are apt to be considerable.

There was a continuous uptake of phosphorus throughout the whole

season, amounting to 30 pounds per acre, with no loss later in the season.

There was a loss of potassium from the plant beginning the latter part of August and continuing until the end of the season. Maximum potassium accumulation of 113.7 pounds occurred on August 22, followed by a gradual decrease till the end of the season. This loss of about 15 pounds of potassium is highly significant.

The total accumulation of calcium during the season was about 12 pounds per acre, with a loss of 1 pound during the latter part of the season.

The total accumulation of magnesium during the season was about 12 pounds per acre, with a continual increase as long as samples were collected. The few slight discrepancies were within the experimental error, so it appears that magnesium is similar to phosphorus in accumulating continually throughout the growing season.

Table IV also shows the accumulation of dry matter and mineral elements in the corn plant during the different periods of growth. Plants 1 month old had accumulated 3.5 pounds of nitrogen per acre and 10 days later on July 1 had accumulated 15 pounds. The highest rate of nitrogen accumulation occurred in the last few days of July, when the average daily intake was 4 pounds per acre. During the grand period of growth, from July 11 to August 4, the daily accumulation averaged 2.7 pounds per acre. A slight drop in total nitrogen on August 28, probably due to the shattering of leaves, was followed by a few pounds additional gain at the very end of the season.

More potassium than nitrogen accumulated during the first 30 days of growth (4.9 pounds vs. 3.5 pounds). This suggests a greater requirement for potassium than for nitrogen as a starter element. The maximum rate of potassium accumulation occurred during the period of July 5 to July 17, when an average of 3.2 pounds per acre entered the plant.

The 30 pounds per acre of phosphorus which accumulated were just as essential to successful growth as were the higher quantities of nitrogen and potassium. Phosphorus accumulation was rather uniform throughout the growing season.

Most of the 12 pounds per acre of calcium accumulated in the leaves and stem and very little in the grain. It accumulated at almost a constant rate throughout the season until vegetative growth ceased.

Magnesium accumulation totaling 12 pounds an acre was also at almost a constant rate throughout the growing season, with very little loss from the tissues. Most of the magnesium, or a large part of it, accumulated in the grain.

The accumulation of dry matter in the plant proceeded at a uniform rate throughout most of the season, but reached a high point about the first of August, when more than 280 pounds of dry matter per acre were accumulated in a single day. Dry matter accumulated as long as the plants were sampled.

Dry matter and mineral accumulation in grams per plant in each of four 30-day periods are shown in Table V. About one-half of the dry weight was produced during the third 30-day period, and the greatest nitrogen and phosphorus accumulation occurred during this same

TABLE V

DRY WEIGHT AND MINERAL ACCUMULATION BY FOUR 30-DAY PERIODS STARTING AT PLANTING TIME ON MAY 20

<i>Period</i>	<i>Dry weight</i>		<i>Nitrogen</i>		<i>Phosphorus</i>		<i>Potassium</i>		<i>Calcium</i>		<i>Magnesium</i>	
	<i>g.</i>	<i>%</i>	<i>g.</i>	<i>%</i>	<i>g.</i>	<i>%</i>	<i>g.</i>	<i>%</i>	<i>g.</i>	<i>%</i>	<i>g.</i>	<i>%</i>
1	5	1	0.15	2	0.013	1	0.21	4	0.022	4	0.008	2
2	122	23	2.35	38	0.341	27	3.18	66	0.255	51	0.241	46
3	243	46	2.86	47	0.596	46	1.43	30	0.225	45	0.244	43
4	156	30	0.76	12	0.332	26	0		0		0.049	9
<i>Total</i>	526		6.12		1.282		4.82		0.502		0.522	

period. The greatest potassium accumulation occurred in the second period and none at all in the fourth period. Some magnesium, but no calcium, accumulated during the last period. About the same proportions of total calcium and magnesium accumulated in the second and third periods of growth.

Losses of most of the elements from the stem, husk, and cob probably were due to movement into the grain. But most of the potassium loss from the leaves, stem, and husk did not move into the grain. Potassium appeared to move back into the soil through the root system. The actual loss is very definite, but more careful studies are required to explain the movement through the plant back into the soil. Very little calcium moves from the husks and cobs into the grain.

V. Mineral Accumulation in Corn Leaves

The composition of the leaves has been studied more extensively than that of any other tissues of the corn plant because they are easier to collect and to study. The leaves reflect the response of the plant to fertilizers better than any other tissues. They can be sampled and studied with little injury to the growing plant. The leaves also are the organs in which most of the organic synthesis of the plant occurs.

Following the development of spectrographic techniques for the

determination of minor elements in plant tissues by Sayre (1944), many studies were made on corn leaves in which the minor elements were determined spectrographically. The results of tests of hundreds of corn leaf samples show that many elements accumulated in the leaves of corn plants. Some of the elements are present in all samples, but others are not. Spectrographic examination of the leaf tissue shows calcium, potassium, magnesium, and phosphorus in every sample. Sulfur does not show on the spectrograph, although it is always present. Copper, silicon, aluminum, boron, manganese, and iron are found in all corn tissues.

The elements so far mentioned are all essential, with the exception of silicon and aluminum. Lead is present in nearly all samples, and silver is shown in more than half the samples examined. Sodium was detected in small quantities in most corn tissues. The tissues from some soil areas show the presence of barium and strontium. Many of the tissues show tin, nickel, and cobalt, and a few of them show chromium. Zinc, which is a necessary element in corn development, is not shown in all samples of leaf tissue, but can be demonstrated as always present in the grain of the corn plant. Molybdenum was not evident in all samples of leaf tissue, but the sensitivity for molybdenum in the spectrograph is not very good. The presence of most elements in the corn tissue undoubtedly indicates their availability or their presence in the soil on which the corn was grown. Their presence may or may not be of any significance to the growth of corn. Under some conditions many other elements present in the soil might be found in corn tissue.

A study of the accumulation of elements in corn leaves during the last half of the growing season was made in 1940, and the results are shown graphically in Figs. 1, 2, and 3. The results are expressed as percentages rather than total quantities, because the leaf tissue mass did not change materially during that part of the growing season.

These data show that the potassium concentration decreases materially during the last half of the season, but that the calcium accumulation is about constant. There is a marked increase in the concentration of magnesium in the leaf tissue, but phosphorus concentration is essentially constant throughout. The amount of boron in the leaf tissue is rather erratic, but there are indications of a considerable increase over the first part of the season when it was not possible to measure boron in some of the samples.

Iron increases in concentration in the latter part of the season. There is a marked increase of manganese in the tissues of the leaves and also a slight increase in copper concentration. Aluminum and silica also increase in the leaf tissue as the season progresses. A summary of these

data indicates that there may be a high accumulation in the leaf tissue the latter part of the season which in the case of some of the elements such as magnesium, silica, boron, and manganese may border on toxicity.

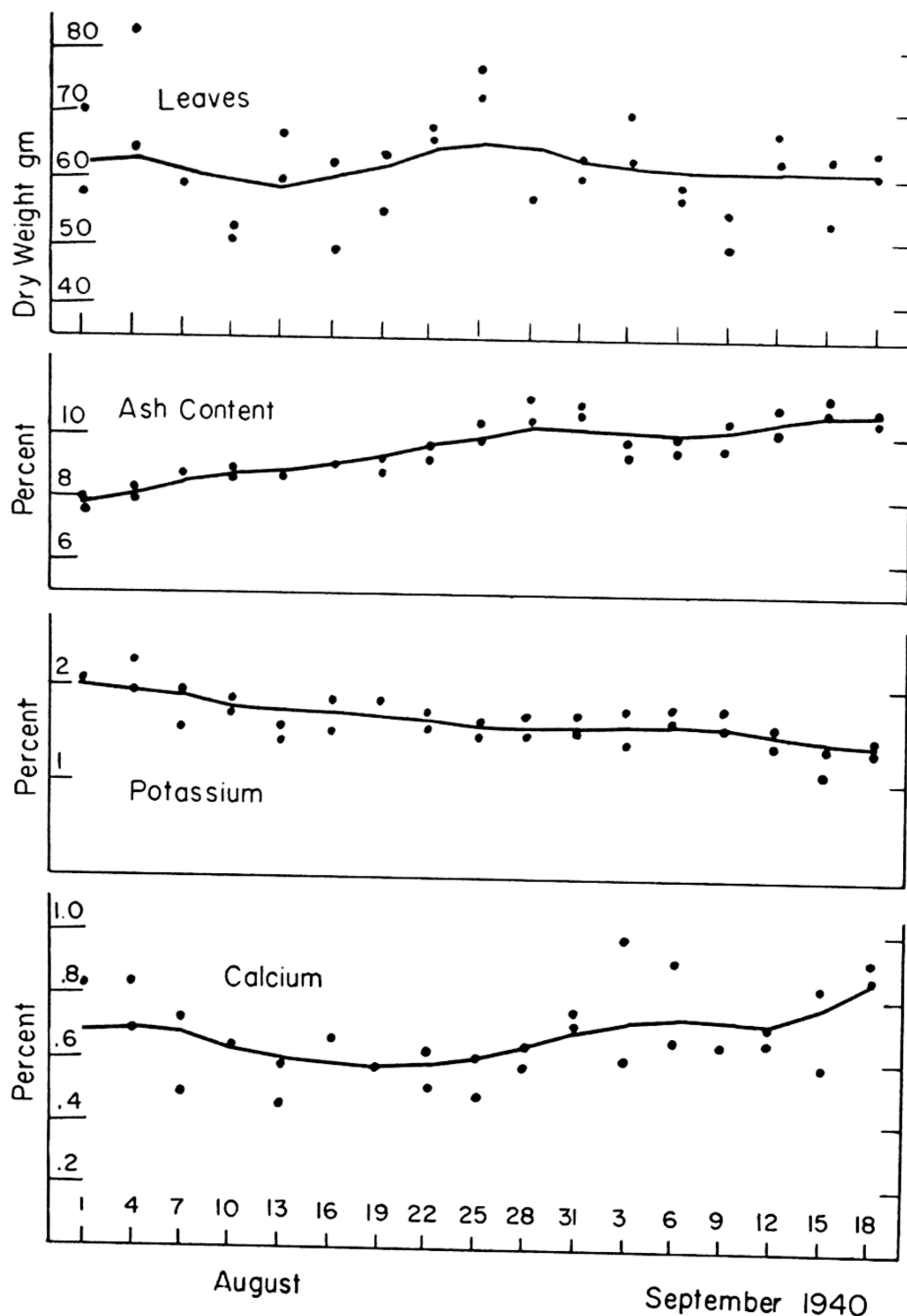


FIG. 1. Dry weight, ash content, and concentration of potassium and calcium in leaf tissue of K35. 1940.

Most of the extensive studies of the seasonal accumulation of mineral elements in corn have been made on double crosses, but many inbred lines that go to make up single and double crosses have been analyzed at certain times during the season. Only a few of the extensive data obtained can be included in this report.

The analyses shown in Table VI were obtained from samples of the ear leaves from 20 plants of each of 13 inbred lines of corn grown on a good soil at Wooster in 1941.

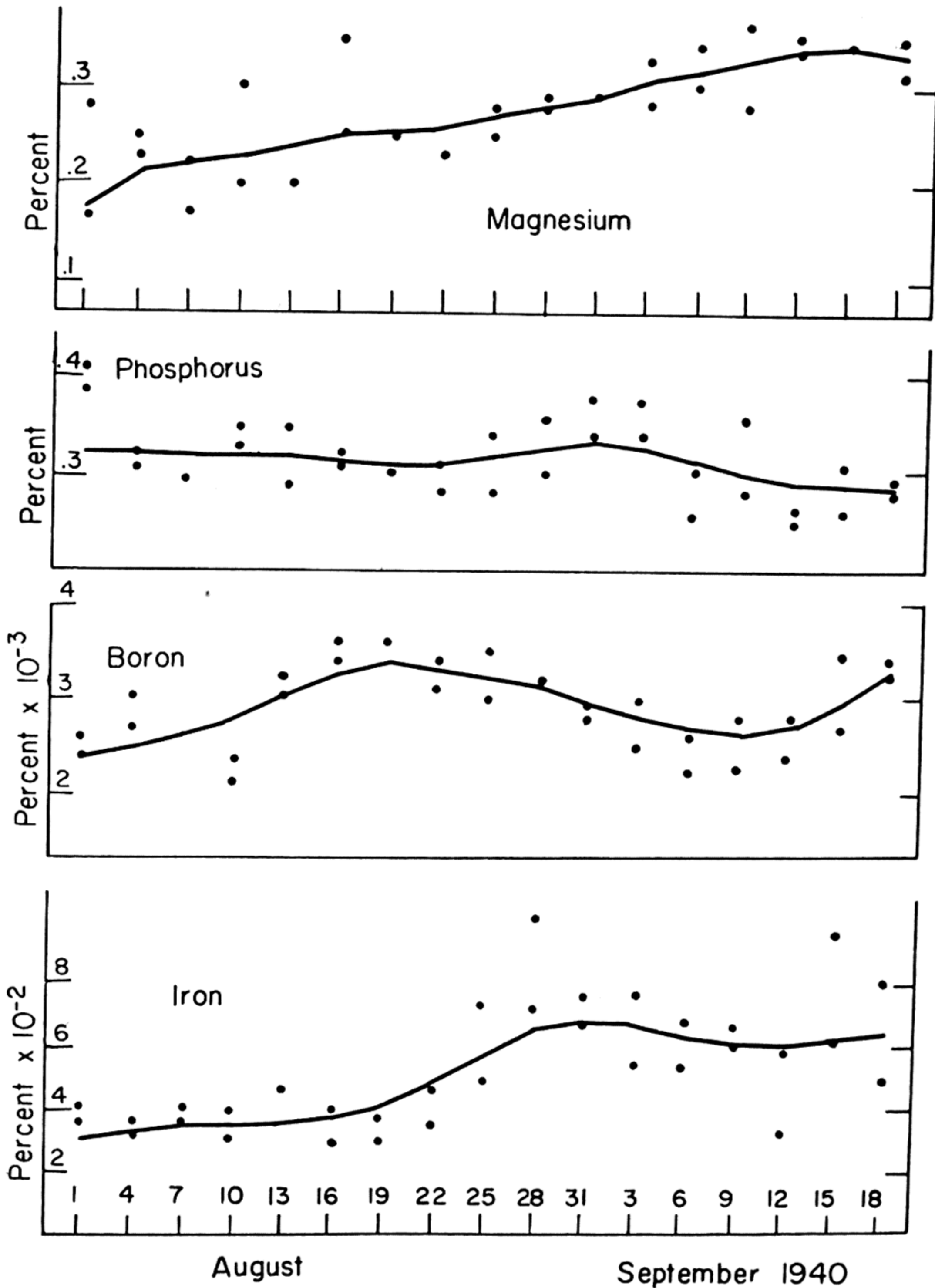


FIG. 2. Concentration of magnesium, phosphorus, boron, and iron in leaf tissue of K35. 1940.

The plants were all sampled at the same time shortly after silking. The analyses were made on dried leaves by ordinary chemical methods. These were mostly Ohio lines which are no longer planted. The data show a wide range in element content among the inbred lines. The content of some elements is twice as high in some lines as it is in others. This indicates that inbred lines of corn have considerably different ac-

cumulating abilities when grown in the same soil under the same conditions.

The results shown in Table VII were obtained from one of the breeding tests at Hillsboro, Ohio, in 1947 where 31 different strains of

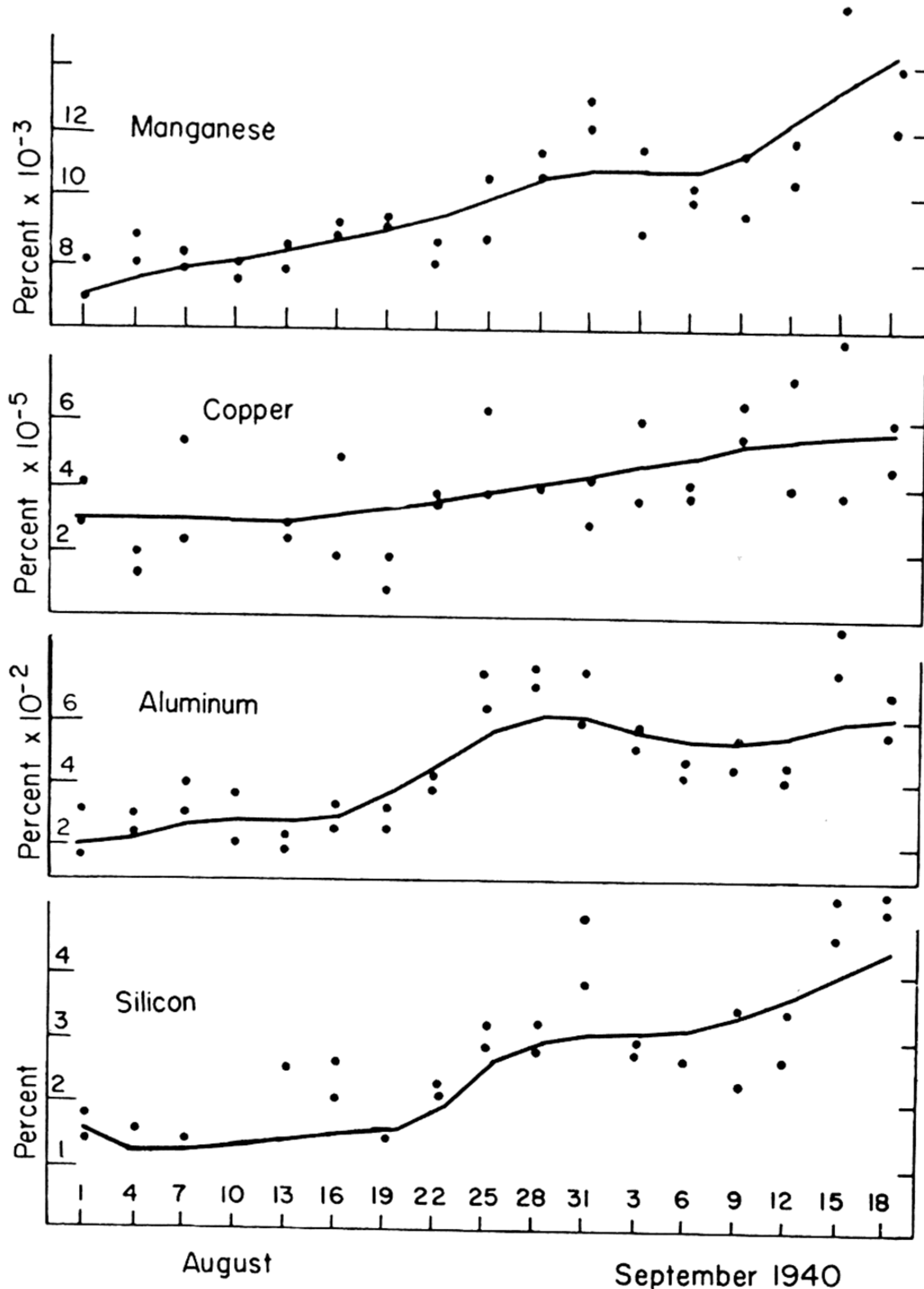


FIG. 3. Concentration of manganese, copper, aluminum, and silicon in leaf tissue of K35. 1940.

corn were being compared. Many of these strains were not inbred lines, but material that was being developed and tested for leaf blight resistance and for possible sources of inbred lines. The data were obtained by spectrographic analysis of the leaf tissue. Ten mineral elements were determined in this set of 31 samples. The values shown in Table VII are relative concentrations of the different elements obtained from

the spectrographic procedure. The determination of relative concentrations, which is much shorter than calculating the percentage composition, is done by comparing the line densities of the different elements recorded on the photographic plate. Such comparisons are valid only for a given element and not between different elements. For example, the amounts of boron and phosphorus cannot be compared because the

TABLE VI

DRY WEIGHT AND MINERAL CONTENT OF EAR LEAVES OF 13 INBRED LINES OF CORN IN 1941

<i>Line</i>	<i>Dry wt. of leaves, g.</i>	<i>N, %</i>	<i>P, %</i>	<i>K, %</i>	<i>Ca, %</i>	<i>Mg, %</i>	<i>Fe, %</i>
Oh02	5.3	2.39	0.263	1.79	0.69	0.24	0.034
Oh40B	6.4	2.27	0.248	1.79	1.17	0.06	0.037
Oh56	5.0	2.46	0.253	2.57	0.77	0.15	0.039
Oh51A	4.2	2.28	0.208	1.93	1.07	0.22	0.038
CC5	6.0	1.82	0.187	1.85	0.94	0.14	0.035
Oh26	4.4	2.39	0.263	0.97	1.30	0.25	0.103
Ind. Wf9	6.0	1.92	0.193	1.98	0.92	0.26	0.032
Oh51	4.0	2.26	0.162	2.05	1.21	0.34	0.038
Oh93	4.5	2.18	0.233	2.13	1.78	0.20	0.041
Oh28	5.5	2.02	0.237	1.81	1.11	0.25	0.036
Oh84	5.3	1.93	0.199	2.02	1.10	0.22	0.037
Oh65	4.0	1.58	0.192	1.89	0.77	0.19	0.043
Oh33	5.5	2.21	0.336	1.72	0.76	0.17	0.053
<i>Range</i>							
Low	4.0	1.82	0.162	0.97	0.69	0.06	0.032
High	6.4	2.46	0.336	2.57	1.78	0.34	0.103

observations are densities of spectral lines of different elements and not concentrations.

These data, and those of many other examinations, show a wide range in the composition of different strains of corn and show that some strains of corn may accumulate much more of certain elements than do others. Since so little is known at the present time of the exact function of all these elements in plants, differences in their content cannot be used extensively in the corn improvement program. All of the above tests were made from randomized field plantings.

1. Radioactive Isotopes and Mineral Elements

New techniques for the study of element accumulation in plants by means of radioactive isotopes have been developed in the past few

TABLE VII

RELATIVE CONCENTRATIONS OF TEN ELEMENTS IN THE LEAVES OF STRAINS OF CORN
GROWN AT HILLSBORO, OHIO, IN 1947

	<i>B</i>	<i>P</i>	<i>Mg</i>	<i>Mn</i>	<i>Si</i>	<i>Fe</i>	<i>Al</i>	<i>Ca</i>	<i>Cu</i>	<i>K</i>
1. Midland S12-1-1-1	0.87	0.87	1.13	1.23	8.1	0.53	0.73	1.50	1.03	1.06
2. " S12-1-1-2	0.82	0.99	1.03	0.97	7.2	0.39	0.60	1.90	0.82	1.07
3. " S27-2-2-1	0.57	0.77	0.61	0.59	3.8	0.52	0.45	0.96	1.4	1.15
4. " S21-1-1-1	0.73	0.74	0.73	0.65	4.6	0.52	0.44	0.96	2.0	1.33
5. " S21-1-1-2	1.04	0.77	0.80	0.64	3.6	0.36	0.39	0.96	1.9	1.03
6. " S21-1-1-5	0.80	0.70	0.72	0.72	3.3	0.43	0.42	0.80	2.3	0.88
7. " S21-1-1-6	0.61	0.70	0.60	0.61	3.2	0.36	0.38	0.56	1.4	0.96
8. " S21-1-1-7	0.82	0.82	0.82	0.75	4.8	0.57	0.48	1.09	2.0	0.82
9. " S21-1-1-8	0.92	0.59	0.65	0.81	3.9	0.75	0.50	1.08	1.8	0.42
10. " S21-1-2-1	1.06	1.27	1.17	1.00	6.9	0.60	0.61	0.90	2.2	1.80
11. " S21-2-3-3	0.88	1.31	1.09	0.81	5.8	0.39	0.66	1.01	1.7	1.42
12. " S21-4-1-2	0.56	0.95	0.73	0.73	2.6	0.33	0.45	0.88	1.8	0.95
13. " S21-4-2-1	0.74	0.87	0.96	0.96	5.4	0.52	0.66	0.88	1.2	0.96
14. (Oh02 × Ind. 38-11)B1-S6-1-2	0.72	1.26	0.92	0.79	4.8	0.39	0.64	0.76	1.9	1.09
15. " " B1-S6-1-4	0.83	1.30	0.98	0.90	6.8	0.45	0.60	0.69	1.9	1.20
16. (Oh04 × CI.14)S1-1-4-1	0.88	1.15	0.70	0.53	5.5	0.38	0.43	1.05	0.8	1.53
17. " " S1-1-4-3	0.77	1.13	0.83	0.52	5.6	0.35	0.51	0.93	1.1	1.50
18. " " S1-1-5-1	0.65	1.10	0.97	0.47	6.2	0.35	0.52	0.98	1.0	1.20
19. " " S1-1-5-3	0.79	1.23	0.70	0.50	4.5	0.28	0.39	1.06	1.1	1.58
20. " " S1-1-5-4	0.62	0.80	0.77	0.53	3.0	0.31	0.44	0.79	1.0	1.28
21. " " S1-1-5-6	0.65	1.41	0.72	0.45	3.1	0.33	0.45	1.13	1.1	1.50
22. " " S3-3-1-1	0.59	1.15	0.88	0.75	4.0	0.30	0.52	0.71	2.8	1.25
23. " " S3-3-1-2	0.50	0.97	0.71	0.65	2.8	0.19	0.40	0.62	2.4	1.23
24. (Oh28 × I159L1)S1-34-1-1-1-1	0.67	0.67	0.67	1.20	4.1	0.33	0.44	0.97	1.2	1.35
25. " " S1-23-1-1-1-1	0.46	0.55	0.50	0.62	2.5	0.31	0.30	0.66	0.9	1.36
26. " " S1-23-1-1-2-1	0.43	0.58	0.52	0.59	2.4	0.32	0.26	0.65	0.9	1.00
27. " " S1-23-1-1-2-2	0.75	0.75	0.64	0.73	3.4	0.29	0.39	0.76	1.1	1.39
28. " " S1-23-1-1-3-1	0.34	0.45	0.45	0.68	1.9	0.27	0.31	0.50	1.2	1.30
29. Oh07	0.70	1.60	1.05	1.60	9.6	0.44	0.65	0.93	1.2	1.18
30. Oh7A	0.85	1.13	0.83	1.41	6.0	0.32	0.47	0.87	1.2	1.22
31. Oh7B	0.76	1.02	0.60	1.19	4.3	0.34	0.41	0.94	0.8	0.80
Range Low	0.34	0.45	0.45	0.45	1.9	0.19	0.26	0.50	0.8	0.42
High	1.06	1.60	1.17	1.60	9.6	0.75	0.73	1.90	2.8	1.58

years. Many of these newer techniques have been used in studying mineral element accumulation in corn. Most of these isotopes are available only in small quantities, and such studies have been confined to small cultures. However, radioactive phosphorus has been available in quantities large enough for field experiments to determine the accumulation of phosphorus from soils (Hendricks and Dean, 1948). The studies reported here have been limited to the elements which were readily available in radioactive form and which lend themselves easily for use in radioactive isotope technique.

The first studies on radioactive isotopes were conducted with phosphorus 32. Many experiments were conducted with corn using this isotope. Radioactive phosphorus, when introduced into a growing corn plant, moves very rapidly to all the tissues of the corn plant and can be detected and measured very easily in most tissues within a few hours. The movement of the radioactive phosphorus into the developing grain can be followed by means of autoradiographs which show its distribution within the grain. Some of the phosphorus was distributed throughout the whole plant, including leaves, stems, and other tissues. Much of the phosphorus accumulated in the grain. It was found throughout the embryo, but in smaller quantities in the endosperm. Most of the information obtained by such studies in gravel cultures had already been determined from chemical analysis. The radioactive isotope technique serves as a convenient check on the results of other more laborious methods. However, in many experiments by other workers where radioactive phosphorus was applied to the soil, much valuable information has been obtained.

A considerable amount of work has been done on the distribution in the corn plant of elements that are not concerned in the metabolism of the plant. Since radioactive isotopes of these elements were readily available, it was thought that their use might bring about a better understanding of what happens in the movement of materials in the corn plant.

A number of these isotopes were obtained and used in gravel cultures with corn, and the results were published by Sayre in 1952 in Bulletin 723 of the Ohio Agricultural Experiment Station. The important result of this study was to show that many of the elements accumulated in very high quantities in the margins of corn leaves. Study of the accumulation of cobalt in corn leaves shows that 40 or 50 times more cobalt accumulated in the margin of the leaves than a quarter of an inch in from the margin (Table VIII). Hoffer and Carr (1923) in Indiana showed that the nodes of the corn plant accumulated high quantities of iron and aluminum and other elements.

Further experiments were conducted to determine the ability of corn leaf margins to accumulate other elements. Some of these experiments were very successful, but others were failures. Radioactive scandium and chromium in low concentrations in dilute acid solutions were introduced into corn cultures in three separate experiments. Neither scandium nor chromium entered or moved to the aerial parts of the corn

TABLE VIII
COBALT CONTENT OF MARGINS AND LEAF BLADES OF CORN, $\times 10^{-8}$ GRAM

<i>Position^a</i>	<i>Margins</i>		<i>Leaf blade, avg.</i>	<i>Ratio avg. margins leaf blade</i>
	<i>Max.</i>	<i>Avg.</i>		
A	14	8.4	—	
B	36	12.0	0.20	60
C	20	14.1	0.24	59
D	38	24.0	1.40	17
E	62	28.0	0.62	45
F	46	28.0	0.40	70
G	32	17.2	0.38	45
H	22	11.0	0.22	50
I	6	4.0	0.16	25

^a The positions are 6-inch sections from the tip to the base of the leaf.

plant in sufficient quantities to be easily detected, as did other radioactive elements such as tungsten, mercury, antimony, and cobalt. These experiments show that the mere presence of an element in the medium in which the plant is growing does not necessarily indicate that it will be absorbed and accumulated in the aerial parts of the plant. Thus, ion absorption can be selective.

2. Marginal Accumulation in Corn Leaves

An experiment to study marginal accumulation of elements was conducted on a group of 31 inbred lines of corn growing under field conditions in a soil of fair fertility. Ten ear leaves of each of the four replications of each line were collected and composited as a single sample and the margins and blades separated. The percentage of margins and blades was determined and a spectrographic analysis of the two types of tissues of each of the inbred lines was completed. The relative concentrations of three of the ten elements which were determined are shown in Table IX.

The data in Table IX show high accumulations of boron in the margins of the leaves. Oh04 shows the least difference in accumulation be-

TABLE IX

ACCUMULATION OF BORON, MANGANESE, AND SILICON IN CORN LEAVES OF INBRED LINES. BADGER FARM, WOOSTER, OHIO, 1951

The values are relative concentrations in the dry tissue

Line	Boron		Manganese		Silicon	
	Blade	Margin	Blade	Margin	Blade	Margin
Oh02	0.12	1.30	0.54	0.97	1.62	1.81
Ind. Wf9	0.08	1.70	0.56	1.29	1.16	1.54
Ill. A	0.10	0.76	0.42	0.99	1.09	0.91
Ill. Hy	0.05	0.80	0.50	1.20	0.97	1.26
Oh51	0.06	0.68	0.62	0.89	1.10	1.35
Oh51A	0.04	0.95	0.37	0.95	1.04	1.67
Ill. M14	0.07	0.93	0.60	0.93	1.20	1.01
Neb. N1	0.05	0.97	0.44	0.82	0.66	0.93
Oh7B	0.07	1.09	0.64	1.19	1.69	2.00
Ia. L289	0.19	1.98	0.56	1.02	1.49	1.79
Wis. W22	0.11	1.03	0.61	1.36	1.25	1.70
Ia. B8	0.20	1.69	0.78	1.16	1.74	2.49
Oh26	0.09	1.68	0.69	1.33	2.18	2.16
Oh07	0.07	1.19	0.95	1.25	2.50	2.53
Oh65	0.10	1.27	0.55	0.58	0.87	0.79
Oh41	0.08	1.24	0.79	1.24	1.29	1.35
Oh56A	0.11	0.78	0.74	0.78	1.65	1.34
Ia. OS420	0.13	2.10	0.43	1.89	1.40	2.02
Ia. OS426	0.10	1.16	0.53	0.90	0.77	0.65
Wis. W23	0.10	1.89	1.11	1.96	1.99	1.77
Ia. L317	0.07	0.67	0.45	0.74	1.07	0.96
Oh29	0.09	1.48	0.62	1.08	1.00	1.05
Oh43	0.18	3.05	0.55	0.84	1.14	1.80
Oh45	0.13	1.96	0.96	1.07	1.54	1.96
CI. 187-2	0.15	1.11	0.65	0.84	1.23	1.37
Oh33	0.07	1.15	0.75	0.61	1.04	0.76
Oh56	0.16	1.57	0.32	1.64	1.94	3.43
Oh28	0.06	1.01	0.55	0.71	0.65	0.68
Oh42	0.10	1.60	0.86	0.62	1.21	1.17
Oh04	0.08	0.26	0.24	0.39	0.90	1.03
Oh40B	0.17	2.71	1.43	4.64	2.58	7.00
Range	Low	0.04	0.24	0.39	0.66	0.65
	High	0.20	1.43	4.64	2.58	7.00

tween margins and blades, a difference of only about 3 times, whereas Oh51A shows a difference of 24 times. The data on manganese show that in two instances or comparisons the blade was higher than the margin. The greatest accumulation of manganese in the margin occurred in Oh56, which had 5 times as much manganese in the margin as in the blade.

TABLE X

SEASONAL ACCUMULATION OF BORON IN CORN LEAVES. OHIO W64. BADGER FARM, WOOSTER, OHIO, 1952

The values are given in p.p.m. of boron in the dry leaf tissue

<i>Date</i>		<i>Blade</i>		<i>Margin</i>	<i>Blade</i>		<i>Margin</i>	<i>Blade</i>		<i>Margin</i>
July	1	7		13						
	8	9		77						
			<i>Upper</i>				<i>Lower</i>			
	15	6		96		9		127		
	22	13		147		7		81		
	29	10		211		7		117		
Aug.	4	22		300		16		203	15	144
	12	16		250		14		170	15	104
	19	22		180		17		115	21	108
	26	32		215		25		162	22	112
Sept.	2	19		185		11		132		27
	9	24		169		22		173		44
	16	16		112		8		90		12
	23	17		76		11		84		14
	30	20		97		17		93		16
Oct.	7	19		70				31		24

Silicon was not accumulated as much in the margins as the other two elements. An examination of the silica values in all the lines shows that in 7 of the 31 instances the margins were lower than the blade. In 6 other comparisons it was approximately equal, and in 18 it was higher in the margins than in the blade. The maximum difference between blade and margin is only about $2\frac{1}{2}$ times instead of 24, as is shown for boron. Results with seven other elements are not shown in this table. In several instances, the margin was actually lower in concentration of an element than the blade. It appears, then, that of the ten elements studied, boron and manganese are quite highly concen-

trated in the margin, whereas others show only moderate or no marginal accumulation in the corn leaf.

In other experiments on marginal accumulation samples were collected every week throughout the growing season from corn plants in a good field and margins and blades were separated to determine the seasonal accumulation as the corn plants developed. Separations or dissections were made by clipping off $\frac{1}{8}$ to $\frac{1}{16}$ of the outer margin of the leaf. The rest of the leaf, without the midrib, was considered blade tissue. The results of this study, shown in Table X, indicate that boron accumulated in the margins of the corn leaf as the season progressed, reached a high point about the middle of the season, and then decreased as the plant matured and the grain was formed.

The upper leaves accumulated more boron in the margin than did the middle or lower leaves. Late in the season the lower leaves could not be separated into margins and blades because of shattering and dying. Boron accumulation in the margins of the upper leaves of the plant increased from about 13 p.p.m. up to 300 p.p.m. and then decreased to about 70 p.p.m. The blade tissues increased slightly in boron content and then decreased to some extent. Accumulation in the middle and lower leaves was less than in the upper leaves. The accumulation of boron in the margins of corn leaves suggests that the boron is required in some of the physiological processes in the leaf. Previous studies of this element in corn nutrition have not shown that it moved about very much in the corn plant.

VI. Summary

The corn plant may produce a large amount of dry matter during the growing season. At maturity nearly half of this dry matter is contained in the grain, which consists largely of starch. Chemical elements are found in all the tissues of corn plants, but the percentage composition of most of them is not very high. The percentage of nitrogen and phosphorus in the embryo of the seed is probably the highest of any tissue in the corn plant. An acre of corn may accumulate 144 pounds of nitrogen, 30 pounds of phosphorus, 112 pounds of potassium, 12 pounds of calcium, and 12 pounds of magnesium. In the various tissues of the plant during the growing season, more than half of the nitrogen accumulates in the grain. There is a continuous uptake of phosphorus during the growing season.

Potassium accumulates in all the tissues of the plant and reaches a high point about the middle of August, then decreases slightly at the end of the season. Calcium is found in all the tissues of the plant, but mostly in the leaves and stems, with only a small percentage in the

grain. A significant loss of potassium may occur from the plant in the middle of August.

The grain accumulates considerable quantities of magnesium. It is found in all of the other plant tissues. Magnesium is absorbed throughout the growing season and may accumulate in the corn leaves. Many elements accumulate in corn leaves and some of them in considerable quantities throughout the growing season, so that they may become toxic to the plant.

Leaves of inbred lines of corn may accumulate two or three times as much of a certain element as do other strains or lines under similar soil conditions.

A very high accumulation of some of the elements was found in the leaf margins through the use of radioactive elements. Spectrographic analysis of leaves of corn growing under normal field conditions showed a very high accumulation of boron and a somewhat lower accumulation of manganese and silica in the leaf margins.

A high point of boron accumulation occurred in the margins of corn leaves about the middle of the season followed by a decrease. The accumulation in the rest of the blade remained about constant during the growing season.

REFERENCES

- HENDRICKS, S. B., and DEAN, L. A. 1948. Symposium on the use of radioactive isotopes in soil and fertilizer investigations. 2. Basic concepts of soil and fertilizer studies with radioactive phosphorus. *Soil Sci. Soc. Amer. Proc.* **12**: 98-100.
- HOFFER, G. N., and CARR, R. H. 1923. Accumulation of aluminum and iron compounds in corn plants and its probable relation to rootrots. *J. Agr. Research* **23**: 801-824. 21 pl., M. 10, 1923 No. 10.
- HOPPER, T. H. 1925. Composition and maturity of corn. *North Dakota Agr. Expt. Sta. Bull.* **192**.
- JONES, W. J., JR., and HUSTON, H. A. 1914. Composition of maize at various stages of its growth. *Indiana Agr. Expt. Sta. Bull.* **175**.
- MEYER, B. S., and ANDERSON, D. B. 1952. "Plant Physiology." D. van Nostrand Company, Inc., New York.
- MILLER, E. C. 1938. "Plant Physiology," 2nd ed. McGraw-Hill Book Company, Inc., New York.
- MILLER, E. C. 1943. Relation between age and dry weight of the corn plant. (*Zea mays* L.) *Kansas Agr. Expt. Sta. Tech. Bull.* **54**.
- SAYRE, J. D. 1944. pp. 1-37. Annual report of corn production, breeding, disease, and quality investigations. B.P.I.S.A.E., A.R.A., U.S.D.A., and Ohio Agr. Expt. Sta. 68 pages, 12 tables, 32 figures. Processed Nov. 1949.
- SAYRE, J. D. 1946. pp. 1-24. Annual report of corn production, breeding, diseases, and quality investigations. B.P.I.S.A.E., A.R.A., U.S.D.A., and Ohio Agr. Expt. Sta. 51 pages, 30 tables, 6 figures. Processed Jan. 1947.
- SAYRE, J. D. 1947a. pp. 1-17. Annual report of corn production, breeding, diseases, and quality investigations. B.P.I.S.A.E., A.R.A., U.S.D.A., and Ohio Agr. Expt. Sta. 105 pages, 23 tables, 31 figures. Processed Dec. 1948.

- SAYRE, J. D. 1947b. pp. 71–105, tables A to T. Annual report of corn production, breeding, diseases, and quality investigations. B.P.I.S.A.E., A.R.A., U.S.D.A., and Ohio Agr. Expt. Sta. 105 pages, 23 tables, 31 figures. Processed Dec. 1948.
- SAYRE, J. D. 1948. Mineral accumulation in corn. *Plant Physiol.* **23** (No. 3): 267–281.
- SAYRE, J. D. 1952. Accumulation of radioisotopes in corn leaves. *Ohio Agr. Expt. Sta. Research Bull.* **723**.
- SAYRE, J. D., GAMMON, N., JR., and CONVERSE, C. D. 1940. pp. 18–35. Annual Report of Studies of the Mineral Nutrition of Corn. B.P.I., U.S.D.A., and Ohio Agr. Expt. Sta., 278 pages, 82 tables, 46 figures. Processed Sept. 1941.
- SAYRE, J. D., and MORRIS, V. H. 1938. pp. 66–80. Results of the cooperative project on corn investigations. B.P.I., U.S.D.A., and Ohio Agr. Expt. Sta. 208 pages, 87 tables, 38 figures. Processed April 1939.
- SAYRE, J. D., and MORRIS, V. H. 1939. pp. 5–19. Results of the cooperative project on corn investigations. B.P.I., U.S.D.A., and Ohio Agr. Expt. Sta. 122 pages, 24 tables, 90 figures. Processed March 1941.

CHAPTER VII

Climatic Requirement

ROBERT H. SHAW

I. Introduction

Corn, because of its many widely divergent types, is grown over a wide range of climatic conditions. Some strains grow very short, others very tall, some require 60 to 70 days to mature, and others require 10 to 11 months. These and other differences among types cause the climatic requirement to vary greatly, and because of this it is difficult to set climatic limits on the areas of corn production. General limits, however, can be set on the major areas.

Relatively few data are available on the specific effects of weather on world corn production; most of the information attempts to define the general areas of production in terms of the climate or climatic regions. Likewise relatively little information is available on the effect of weather on specific periods of plant development. The bulk of the information concerns the effect of weather on the yield of corn and is related particularly to the Corn Belt of the United States.

II. World-Wide Corn Production and Climate

Among the workers who have attempted to define the limiting climatic conditions for corn production are Finch and Baker (1917); Ward (1919); Wallace and Bressman (1937); Jenkins (1941); and Klages (1942). This work has shown that general limits can be determined with respect to low precipitation and low temperatures, but no definite limits have been determined for high temperatures and high precipitation. Corn is a warm-weather plant. Practically no corn is grown where the mean summer temperature is less than 66°F. or where the average night temperature during the three summer months falls below 55°F. The region of greatest production in the United States is the area with a mean summer temperature of 70°F. to 80°F., a mean night temperature exceeding 58°F., and a frostless season of over 140 to 150 days. Corn is grown at practically all latitudes except where it is too cold or the growing season too short.

Corn is grown in areas where annual precipitation ranges from 10 inches to over 200 inches. A summer rainfall of 8 inches is about the

lower limit for corn production without irrigation, although if evaporation is not excessive an even smaller summer rainfall will suffice. In the best corn areas of the Corn Belt 5 inches of rain occur during the 50-day period centering around tasseling. Corn can be grown in areas with very heavy precipitation, as shown by the production in parts of India and Java, but under very low rainfall conditions it must be grown under irrigation.

III. Climatic Regions of Corn Production

The bulk of the corn crop (Fig. 1) is grown in climatic regions transitional between marine and continental, and in sections either with distinct woodland climates or climates transitional between woodland and grassland. Corn production is limited in areas where the native vegetation was short grass, but is an important crop in areas native to tall grasses.

In the United States the heart of the Corn Belt is located in a mesothermal or warm temperate climate with a warm summer and no distinctly dry season; at least eight months have an average temperature above 1°C. (33.8°F.) (Köppen, 1931; Goode, 1939).

The so-called Cotton Belt, a humid mesothermal climate, also has no distinctly dry season and grows large amounts of corn.

In a humid microthermal or cool temperate continental climate with cool summers, such as the area north of the Corn Belt, some corn is grown, but it is often too cool, or the frostless season is too short, and corn may be subordinate to other crops which are more profitable. In this area at least four months have average temperatures under 1°C. (33.8°F.).

In the dry, middle-latitude, steppe climate west and northwest of the Corn Belt, midsummer moisture demands of the corn may be too great, and wheat and barley become more important because they can complete their cycle before dry weather arrives.

In Argentina the bulk of the corn is grown in a sub-humid mesothermal or temperate climate with a warm summer and no distinctly dry season. Where corn is grown in the dry steppe region, yields fluctuate widely because of extreme variations in rainfall. In Brazil corn is grown either in a mesothermal climate with a dry season in winter or in a tropical climate which has relatively constant temperatures with a dry winter season.

The areas of corn production in China are very similar to those of the Corn Belt with respect to a mesothermal climate; they differ, however, in that the winters are a distinctly dry season. Compared with that in the Corn Belt, rainfall during the growing season is the same or slightly heavier.

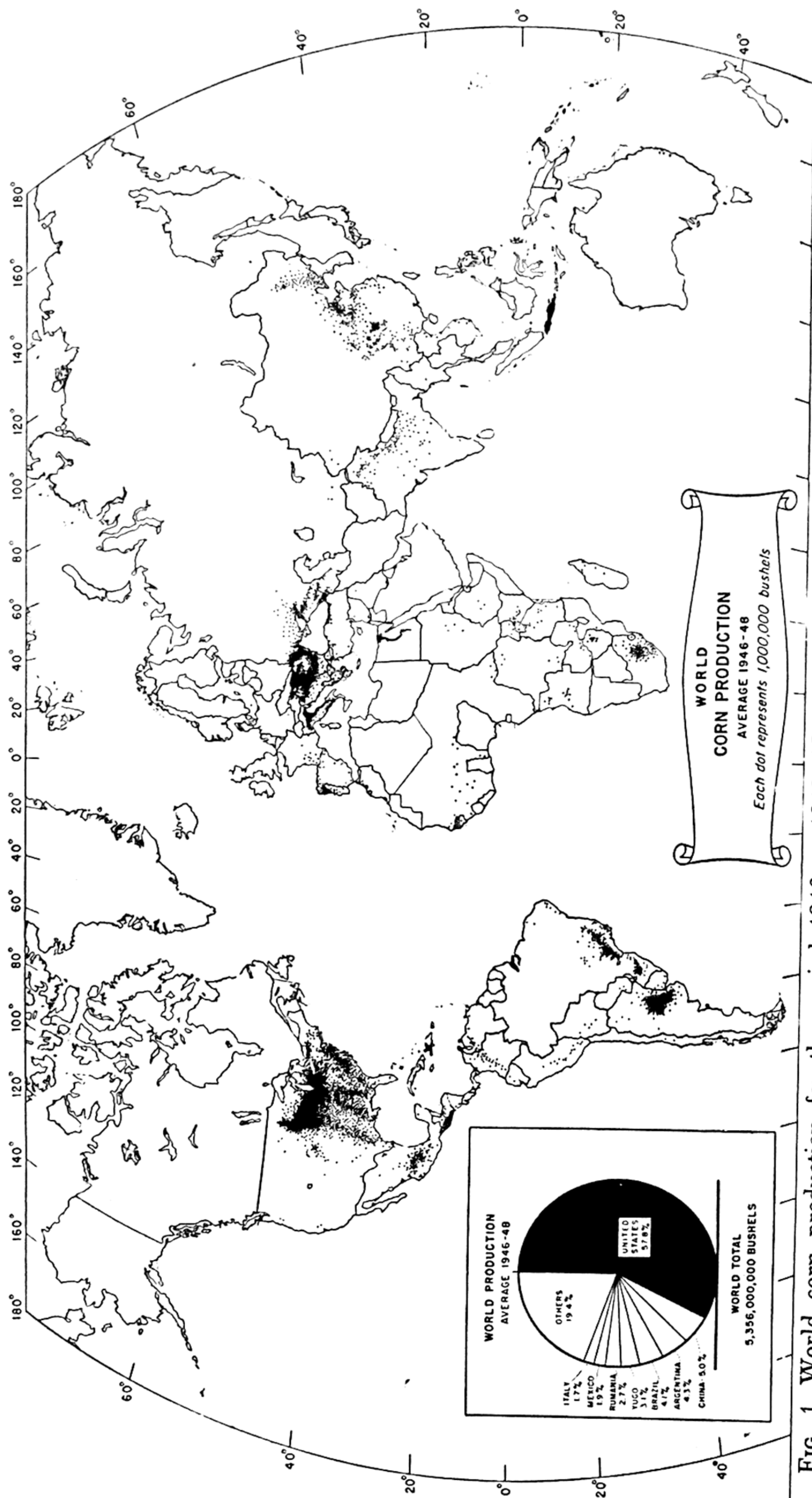


Fig. 1. World corn production for the period 1946 to 1948 (Courtesy Office of Foreign Agricultural Relations; U.S. Department of Agriculture).

The areas of corn production in the Balkans and Italy are largely either mesothermal climates with no distinctly dry season, or mesothermal climates with summer as a dry season. Precipitation is similar to that in the area just west of the Corn Belt, with the result that yields may be reduced because of lack of moisture. In the steppe regions of Roumania wheat and barley become more important because of summer dryness.

In Russia corn is grown largely in a steppe climate where moisture may be somewhat limiting. Some corn is grown also in a relatively cool, moist microthermal climate.

Other areas of corn production are India, where corn is grown in a mesothermal climate with a dry season in winter owing to the monsoon circulation present in that country; Java and part of the East Indies, where corn is grown in a moist tropical climate with the winter as a dry season; Mexico, in areas ranging from a dry steppe climate to a moist tropical climate; and in South Africa, in a mesothermal climate or a steppe climate with dry winters and relatively cool summers.

IV. Effect of Weather on Certain Periods of Plant Growth

1. Prior to Planting

The influence of weather on the corn plant starts even before planting. Conditions before planting are especially important in determining soil moisture reserves and the time of seedbed preparation. Little quantitative work has been done, however, in determining the effect of weather in this period on subsequent corn growth. Although some soil temperature data are available, they have not been analyzed prior to the time of germination and seedling growth. Newlin (1948) pointed out that a deep freeze in the winter is important in getting the soil in good condition and in reducing clods and packing by machinery or animals. Spring rains which help replenish soil moisture reserves may also delay field operations, whereas warm sunny days hasten field operations. Spring weather is important in determining the time at which field operations can be started.

2. Planting to Emergence

Kincer (1919) found that the average temperature at the time when corn planting began varied from 54° to 57°F. in most of the areas where corn was grown in the United States. This varied from early February in the South to the middle of May in the North. However, this repre-

sented only the early fields, and was not necessarily the time when most of the corn was planted. Data collected by the Weather Division, Iowa Department of Agriculture (1949), showed that the average date of planting in Iowa, for a 31-year period, was May 15. On a yearly basis, this has varied from May 10 to May 22, with weather the principal factor determining the time of field operations. The average temperature for Iowa at this time is about 60°F., which is very close to the average of 61°F. cited by Wallace and Bressman (1937) as the temperature prevailing at the time the bulk of the corn planting is done.

This period from planting to emergence is characterized by a dependence on soil temperature, soil moisture, and seed stored food. Before germination the seed imbibes water and swells. Water must be available for imbibition and subsequent seedling growth. A suitable temperature must be present for both germination and later growth to take place. The time from planting to emergence varies widely with environmental variations.

In tests using a silt loam soil, Wolfe (1927) found that the rapidity of germination increased with increased soil moisture up to 80 per cent of saturation. At 10 per cent saturation there was no germination owing to lack of water, whereas at 100 per cent saturation or above germination was retarded or prevented owing to lack of oxygen. On a silt loam soil held at 50 to 60 per cent moisture, a temperature of 35°C. (95°F.) gave slightly more rapid germination than one of 30°C. (86°F.) and considerably greater rapidity than one of 25°C. (77°F.).

In the greenhouse, corn has sprouted in 4 days when at a temperature of 80°F. In the field at Ames, Iowa, corn has emerged in an average of 7 to 15 days in a six-year period. According to Wallace and Bressman (1937), at an average temperature of 60° to 65°F., corn usually appears above the ground in 8 to 10 days, whereas at 50° to 55°F. it takes 18 to 20 days. If the soil is moist and at a temperature of 70°F., emergence may occur in 5 to 6 days.

The growth rate before and immediately after emergence can be estimated from Lehenbauer's (1914) oft-cited work. However, it should be remembered that his work on maize seedlings was carried out in a humid-air environment, in almost total darkness, and at fixed or quickly changed temperatures. He found that growth rate varied both with temperature and with length of exposure to a given temperature. Using average hourly growth rates for 3-hour periods Newhall (1947) developed an exponential curve by the method of least squares to provide a measure of the growth rate.

$$G = K \left(\frac{T - 10.5}{10} \right)$$

where G = growth rate (mm./hr.) $\times 10^{-1}$;

$K = 3.35$;

T = temperature, $^{\circ}\text{C}$.

The lower limit below which it was assumed that no growth occurred was arbitrarily chosen at 2°C .; the upper limit, above which it was assumed that growth was essentially constant, was 29°C . and was obtained by an approximation of Lehenbauer's actual experimental results.

Another factor which should be considered is that in many studies air temperatures are used, even though the soil is the medium in which the seedling starts. Newhall (1947) found that for central Iowa the average soil temperature for April 15 to June 15 at planting depth was slightly higher than the standard air temperature.

Using growth rates computed from the exponential growth curve and soil temperature data collected in the field he found a correlation of 0.96 with the observed growth rates. On two other years of data the correlation was 0.92 and 0.95.

Irwin (1931), using accurately measured soil temperatures, found a high correlation between temperature and the emergence interval on several crops, although corn was not included in his observations. When soil temperatures were not available, and adjacent air temperatures were used, Newhall (1947) found correlations to be much lower. When data were used for areas not in the immediate vicinity of the weather station, the correlations were erratic. Daily readings gave higher correlations with the emergence interval than did the average or average maximum temperature during the growth period.

The work of Newhall (1947) showed that soil temperature "closely follows" air temperature, i.e., there is little accumulation in the earth. The soil may be much warmer during periods of intense heating, but on cloudy days soil temperature at planting depth closely approximates air temperature. In practical application this means that bright warm days in April do not "heat up the ground" for rapid corn emergence in May. In order to have a short emergence interval, daily heating of the soil must prevail during the period of germination and seedling growth.

There are other important aspects of the effect of weather to be considered. Cold wet weather following planting favors the development of pathogens. Numerous investigators have shown that various pathogenic organisms are capable of causing kernel rot and seedling blight under conditions of low temperatures, and particularly where the soil is of a rather high moisture content. Time of planting may be altered in an attempt to reduce insect injury, but this may increase injury from

pathogenic organisms. Tatum (1940) presented data which indicated that growers should proceed with caution in following recommendations for earlier than normal planting because of dangers of disease injury to the seed in the ground. At temperatures a little above freezing (33°F.), corn which had not had a chance to germinate remained alive and healthy for a relatively long time. When allowed to germinate for two or three days before being subjected to low temperatures, the young plants were nearly all killed by a few days of exposure. Death at this time was probably due to a change in the physiology of the corn seedling because of the low temperatures, rather than to damage from pathogens. At temperatures just low enough to prevent growth of corn or to allow growth at a slow rate (around 45°F.) the injury was probably due to harmful organisms which could grow and readily attack the dormant seeds, whereas those which had germinated tended to be more resistant. His results also indicated that stands were poorer from early plantings. Dungan (1944) pointed out that in view of the detrimental influence of late planting on the yield and quality of the crop it appeared that the use of this method for the reduction of insect and disease damage should be adopted with caution. In the South, Johns and Brown (1941) found that date of planting was important in determining the amount of damage by southern corn rootworms and corn borers.

Rush and Neal (1951) found that low temperatures (46° to 54°F.) retarded the physiological activities of germinating corn kernels and predisposed them to attack by various soil organisms. Their data indicated that frost injury and maturity of seed at time of harvest were important factors in determining stands of corn at low temperatures.

3. *Emergence to Tasseling (Vegetative Growth Period)*

Shortly after emergence, an important change takes place when the plant changes from one of dependence on stored food to one of self sufficiency. During the early part of its life the corn plant requires a limited amount of moisture for the small growth that takes place. If the weather is somewhat dry at this time, the roots will penetrate deeper into the soil, and the plant seems better able to withstand later dry weather.

Young corn plants are relatively resistant to cold weather, with a temperature of 30°F. generally killing exposed above-ground parts (Shaw, Thom, and Barger, 1954). Hanna (1924) found that 29°F. injured corn and 24°F. killed the corn. Holbert and Burlison (1929) found that certain inbreds and hybrids among them, when 4 to 6 inches high, escaped apparent serious injury with temperatures as low as

25°F., whereas other inbreds and hybrids were killed at these same temperatures. A late freeze of 31°F. in 1947 in central Iowa, accompanied by snow, killed above-ground parts of many plants, but recovery was rapid.

In corn plants two to three weeks old, Sellschop and Salmon (1928) found that chilling had no marked immediate effect. From 5 to 10 days after chilling light yellow bands developed on the leaves, which became filmy and rust colored toward the edges. Bands occurred on those parts of the blades which formed the whorl of the plant at the time of the chilling. In this region the most active growth takes place and the youngest tissues are found. In general, the younger the plant, the greater the injury. Plants six weeks old, chilled at temperatures of 0.5° to 5°C. (33° to 41°F.) for different lengths of time, recovered and were capable of seed production if less than 25 per cent of the area was recorded as showing injury soon after chilling. With 25 to 50 per cent injury plants occasionally recovered, whereas those injured more than 50 per cent seldom recovered. As the length of chilling increased the amount of injury also increased. In a saturated soil greater injury occurred than in a moderately wet soil, with least injury in a moderately dry soil.

In semiarid areas high temperatures may be a major factor in limiting crop production. Hunter, Laude and Brunson (1936) and Heyne and Laude (1940) found that seedlings 10 days old were very resistant to high temperatures, at 14 days they were slightly less resistant, and at 16 to 20 days, they were very susceptible.

Growth during the vegetative stage has been found to be related to both temperature and rainfall. Bair (1942) found that the correlation between increments of growth, expressed as dry weight gain of the total plant, and the physiological indices of Lehenbauer (1914) was 0.81 in 1939, but only 0.26 in 1938. A poor distribution of rainfall was believed the cause of the poor correlation in 1938. Hanna (1925) found the growth of corn more closely correlated with temperature than with any other single climatic factor. Growth gave the best correlation with temperature when remainder indices above 10°C. were used. Variations in temperature alone have accounted for 40 to 70 per cent of the variability in growth rates (McCalla, Weir, and Neatby, 1939). Under conditions of low moisture, plant growth was checked and root development stimulated (Loomis, 1934). He found that growth of maize depended upon a liberal supply of water at the growing point. In order of effectiveness such a supply was reduced and growth checked by (1) direct sunlight, (2) deficient soil moisture, and (3) low relative humidity. Growth rate decreased rapidly as the temperature approached 10°C.;

this is probably largely due to slowing of chemical processes of cell division, but may in part be due to decreased rate of translocation of food materials. Most rapid growth was made in the late afternoon and early evening and morning, or on cloudy days when the air temperature was high and a water deficit was not maintained within the plant shoot by a high transpiration rate. In general, the growth rates followed the temperature curve at night and the moisture supply curve, as partially indicated by the relative humidity of the air, during the day.

Kiesselbach (1950) in computing average daily growth over a three-year period, during the time of rapid vegetative development, found almost the same amount of growth during the daylight hours as at night. Average daily growth, as measured by height to the tip of upstretched leaves, was 2.51 inches, with 7 A.M. to 7 P.M. growth 1.23 inches and 7 P.M. to 7 A.M., 1.28 inches. For specific temperatures and assuming moisture was not limiting, Wallace and Bressman (1937) estimated daily growth rates ranging from 3.2 inches at a temperature of 65°F. to 5.4 inches at a temperature of 78°F. However, under many conditions moisture may be limiting, and as pointed out by Haynes (1948), the quantity of vegetative growth was markedly affected by the degree of availability of soil moisture, even though within the range from near saturation to near permanent wilting the amount of water transpired per unit of plant dry weight produced was not.

4. Time of Tasseling and Silking

The temperature previous to this time is very important in determining the time of tasseling. Wallace and Bressman (1937) cite data showing that a so-called 115-day strain took 74 days from planting to tasseling at an average temperature of 68°F., whereas it took 54 days at an average temperature of 73°F. A 90-day strain took 59 days at a temperature of 67°F. and 43 days at a temperature of 71°F. Other data of Shaw and Thom (1951a) substantiate this same pattern.

Hutcheson and Wolfe (1919) found that the time from the appearance above ground to tasseling was also changed by moisture conditions. Plants grown to tasseling in a soil 70 per cent saturated took almost two weeks less time to tassel than did those grown at 40 per cent moisture. There was little difference in the time from tasseling to silking under the different moisture conditions.

After tasseling starts heat no longer plays such an important part. It seems that hot weather does not have nearly as much to do with hastening ripening as it does with causing rapid growth before tasseling. Cool nights reduce the rapidity of growth previous to tasseling. A difference of 8 degrees in temperature for the 60 days after planting

caused a variation of almost a month in time of tasseling (Wallace and Bressman, 1937). Each degree the temperature averaged above 70°F. for the 60 days speeded up tasseling 2 to 3 days. Shaw and Thom (1951a) found that in a hot dry year the rate of silking was much slower than in a normal year.

Although it is evident that weather affects the time of tasseling and silking, there has been little success in predicting silking from weather data. For the period 1921 to 1945 data of the Iowa State Department of Agriculture (1949) show that the interval from planting to first silking averaged 65 days for Iowa, with a range of 20 days. Much of this variability occurs in the interval from emerging to tasseling. The length of this interval varies considerably both among years and among varieties.

Decker (1947) found that mean daily rainfall was not correlated with the length of the vegetative period. This may be partially due to the fact that it is not a satisfactory indication of the amount of moisture present in the soil. Date of planting itself is not a good value to use in predicting the silking date, and, as shown by Mangelsdorf (1929) and others, the period between planting and silking may be shortened if planting is delayed. Decker (1947) found that the mean temperature may be used, but the type of season affects the slope of the regression line if used in predicting silking dates. The mean temperature for the 30 day period after planting was the best indicator of the length of the vegetative period and was better than the mean temperature taken over the entire period. Best results were obtained when the effect of the planting date was removed. As the planting date changed, the slope of the regression lines of days to silk plotted against temperature changed. Using the regression lines as developed by Decker (1947) for central Iowa, on data taken in 1947 and 1948, Shaw (1949) found predicted silking dates 3 days late in 1947 and 9 days early in 1948. A drought near tasseling and silking time may delay silking in relation to tasseling (Shaw, 1949; Kiesselbach, 1950) and may result in tassels being partly sterile and in a large percentage of barren or nearly barren stalks (Loomis, 1937).

Fertility level as well as weather affects the time of tasseling or silking. Time of silking was frequently hastened 4 to 10 days by the addition of fertilizer (Dumenil and Shaw, 1952) and in an extreme case was hastened 30 days. The interaction of fertilizer and weather complicates the problem of predicting silking dates for field corn.

5. *Maturity*

Although the length of the period prior to silking is very sensitive to weather, some work has indicated that the period from silking to

maximum dry weight is relatively independent of weather variations (Brown and Garrison, 1922; Iowa State Department of Agriculture, 1949; Shaw and Thom, 1951b). It seems this period is sufficiently constant regardless of the weather, to have a forecasting value in relation to frost damage. In Iowa it has been found the average length of the period is 51 days, with a relatively small variation.

The rate of drying of corn is influenced by weather. General statements can be made, but quantitative field data are lacking. It is generally believed that increased wind, sunshine, and warm dry days increase the rate of drying, but the quantitative effect of each under field conditions is not too well known.

As corn approaches maturity it may be subjected to freezing weather or frosts. Holbert and Burlison (1929) found that some inbreds were killed by a few hours of air temperatures of 45° to 50°F., and many were killed by a succession of cold nights of 33° to 45°F. Some withstood temperatures of 28°F. Most commercial varieties in the Corn Belt are able to withstand air temperatures above 32°F. with little, if any, injury.

V. Effect of Rainfall and Temperature on Yield

As one might expect, by far the greatest amount of work has been done in determining the effect weather has on the yield of corn.

The development of the corn plant can be divided into five reasonably distinct stages, each with its own response to weather and its own relation to final yield (Hershey, 1934; Paddick, 1944). These stages are: (1) early vegetative growth from planting to flower differentiation; (2) rapid vegetative growth from a plant height of about 50 cm. to silking; (3) pollination and fertilization; (4) grain production from fertilization to maximum dry weight of the grain; (5) maturation or drying of grain and stalk.

The first development stage (Shaw and Loomis, 1950) includes germination, the seedling stage, and early leaf growth during the three to four weeks of independent development. At the end of the period the plants are about knee high and the maximum number of leaves, vascular bundles, and ovules on the embryonic ear shoots are already determined. The potentialities of the plant are established during May and early June in the Corn Belt, and this period is of great theoretical importance in yield prediction. Actually, however, weather is seldom limiting during this period in much of the Corn Belt, except as it affects stand; and soil fertility is the major factor. Because the corn plant seldom reaches its maximum potentialities under field conditions and has extensive powers of recovery from early season setbacks, it is diffi-

cult to predict yields from early season observations. During the second period the leaf area of the plant increases from 5 to 10 times and the weight of the culm 50 to 100 times. At the end of this period the size of the organs has been determined and maximum stalk height, stalk diameter, and leaf area may now be measured.

Ear shoot development, pollen formation, and fertilization may be considered in the third phase—an important one in production of the corn crop, although it will not be discussed here.

The first part of the grain production period consists of about three weeks of rapid growth of ear shoot, husks, cobs, and young kernels. Growth during the next four to five weeks consists largely of an increase in dry weight of the developing kernels. Up to 85 per cent of the dry weight of the grain may be produced in this last period. This period should be less sensitive to weather factors than preceding periods because it involves less cell division and a lower level of physiological activity. Photosynthesis is not likely to be reduced below normal unless the plants wilt during the day (Verduin and Loomis, 1944) or the lower leaves fire because of droughts or mineral deficiencies. With this physiological material as a background the effects on yield are discussed.

1. Calendar Periods

The material covered by calendar periods is almost entirely restricted to the Corn Belt or comparable latitudes. For comparison in other areas it must be related to the stage of development of the corn plant.

a. May. As the previous discussion would indicate, weather conditions during early stages of growth have less effect on yield than conditions at later stages of development. Early spring rains in many areas may be beneficial in building up soil moisture reserves, although Pengra (1946) found that preseasonal precipitation in the northern Great Plains showed a correlation of only 0.36 with corn yields.

During May much of the corn is planted, and germination and some early leaf growth may take place. The relationship found between May temperature and yield has varied widely in different studies. The effect of planting dates on this relationship has been largely neglected, probably because of the relatively common planting dates for the Corn Belt. Wallace (1920) found low correlations between May temperature and yield. He estimated that an average May temperature of 60°F. in central Iowa resulted in average yields, whereas at 55°F. the yield was reduced 15 per cent. Temperatures above 60°F. increased yields slightly. Rose (1936) also found correlations relatively low for May temperatures. His results show that May temperatures in the north and northeast sections of the Corn Belt were positively correlated with yield,

whereas in the southwest section there was a negative correlation. Areas in which higher than average May temperatures resulted in lower than average yields were those having May temperatures of 61°F. or above, and those where higher than normal temperatures gave higher than average yields averaged below 59°F. For Indiana, Visher (1940) found a positive relation between yield and temperature. However, Davis and Harrell (1941) found that higher early May temperatures in Ohio were detrimental to yield, but in the southwest part of the Corn Belt positive correlations were found.

In the western section of the Corn Belt Wallace (1920) and Rose (1936) found that increased yields resulted from increased rainfall, but Davis and Harrell (1941) found that increased precipitation in Nebraska in early May resulted in decreased yields. Wallace (1920) estimated that May rainfall above 5 inches resulted in decreased yields. Visher (1940) found that May precipitation should be heavier than the normal of 4 inches and be accompanied by increased temperature for optimum yields in Indiana.

In general, spring rains in most of the Corn Belt, especially in the southwest in Kansas and Nebraska, are beneficial to the corn crop because they build up moisture reserves in the soil. Statistical studies do not reveal a high relationship with yield. In much of the corn-growing area rainfall is adequate through early stages of development. Root development and soil nitrification are both favored by a warm, moist, well-aerated soil.

b. June. In June, when higher temperatures are becoming more prevalent, the western part of the Corn Belt, and in particular the sub-humid southwest section, showed negative correlations between temperature and yield (Wallace, 1920; Rose, 1936; Davis and Harrell, 1941). Accumulated temperatures above 90°F. also showed a negative correlation with yield, but in Ohio and bordering areas the correlations were positive. Visher (1940) also found that temperatures slightly above average resulted in higher yields of corn in Indiana but that temperatures considerably above average were detrimental. Higher temperatures during early June also gave higher yields in Maryland and Pennsylvania. Presumably, the corn crop in the relatively humid northeastern part of the Corn Belt would be benefited by more heat than it commonly receives during the early periods of growth.

Wallace (1920) estimated that corn yields in central Iowa were normal for average June temperatures of 68° and 72°F., slightly above normal for temperatures 69° to 71°F., and below normal for average temperatures below 68°F. and above 72°F.

In the southwest part of the Corn Belt increased rainfall during June

gave increased yield (Wallace, 1920; Rose, 1936; Davis and Harrell, 1941), but in other parts of the Corn Belt results have been conflicting or indecisive.

Davis and Pallesen (1940) found that early in the season mean rainfall in Ohio was above optimum but by late June this was not so. Hendricks and Scholl (1943) found that for rainfall amounts below $1\frac{3}{4}$ inches in Indiana and $4\frac{1}{4}$ inches in Iowa the average effect of 1°F. increase in temperature was a decrease in yield. With rainfall above these amounts in Indiana and Iowa, and for all amounts of rainfall in Ohio, the average effect of a 1°F. increase in temperature was an increase in yield. The "critical values" for different months are given in Table I.

TABLE I

AMOUNT OF PRECIPITATION, IN INCHES, ABOVE WHICH INCREASED TEMPERATURE
GAVE INCREASED YIELD, AND BELOW WHICH INCREASED TEMPERATURE
GAVE DECREASED YIELD
(Hendricks and Scholl, 1943)

<i>Month</i>	<i>Ohio</i>	<i>Indiana</i>	<i>Iowa</i>
June	All positive	1.6	4.3
July	6.8	4.3	4.3
August	1.8	All positive	2.7

Yield increases were relatively small in June compared to other months, the greatest increase being slightly over 1 bushel per degree F. increase in average monthly temperature.

In a like manner Hendricks and Scholl (1943) determined critical levels of temperature for varying amounts of rainfall (Table II). For

TABLE II

TEMPERATURE ABOVE WHICH INCREASED PRECIPITATION GAVE INCREASED YIELDS
AND BELOW WHICH INCREASED PRECIPITATION GAVE DECREASED YIELDS
(Hendricks and Scholl, 1943)

<i>Month</i>	<i>Ohio</i>	<i>Indiana</i>	<i>Iowa</i>
June	63.8	67.6	70.8
July	47.8	69.7	72.3
August	69.3	61.8	69.1

average temperatures below 63.8°F. in Ohio, 67.6°F. in Indiana, and 70.8°F. in Iowa, the effect of an increase in rainfall was to decrease the yield, whereas at temperatures above these values the average effect of an increase in rainfall was to increase yields.

c. July. In the Corn Belt corn grows very rapidly during early July. In early July much of the corn is starting on the period of rapid vegeta-

tive growth. In most years the corn is largely silked by the end of July. Wallace (1920) found that in most states July temperature was negatively correlated with yield. Rose (1936) found that in the northwest, southwest, and southern margins of the Corn Belt the correlation was negative. It would seem that the temperatures are too high during this period in the areas where moisture is usually not too plentiful. In the central part of the Corn Belt he found little correlation. Davis and Harrell (1941) found that increased temperature resulted in decreased yields in Pennsylvania, Maryland, and the Corn Belt with the exception of Illinois. Hendricks and Scholl (1943) found that with increasing amounts of rainfall yields were increased by higher temperatures. However, the critical points were much higher for July than for June rainfall (see Table I).

Moisture is more likely to become limiting in July. Because of this, July rainfall was more frequently correlated with yield than was rainfall for previous months, and most of the Corn Belt showed highly significant correlations with yield.

Hendricks and Scholl (1943) found that in general the increase in yield due to increased precipitation, especially at higher temperatures, was much greater than in June. For the total precipitation, April through July, Wallace (1920) estimated that for central Iowa 10 inches gave a normal yield and that yields decreased with less precipitation and increased with more precipitation. This takes no account of the seasonal distribution of precipitation. He also studied the relationship of July rainfall and temperature with yield and found that for 1 inch or less of rainfall yields were always below normal, from 1 inch to 3.5 inches best yields were obtained with an average temperature of 71°F., and with 4 inches or more highest yields were obtained at higher temperatures. Only with 6 inches or more of rainfall and low temperatures were below-normal yields obtained.

d. August. In August temperatures in much of the Corn Belt may normally be too hot for best corn yields (Wallace, 1920; Rose, 1936; Davis and Harrell, 1941; Kiesselbach, 1950). Temperatures in the western part of the Corn Belt may be critical. A greater frequency of temperatures below 60°F. in many areas is likely to give higher than average yields. Along the entire south margin of the Corn Belt high August temperatures seem unfavorable for yield. In the humid eastern part of the Corn Belt or the northern border some data indicate that the corn may suffer slightly from lack of heat. In central Iowa, Wallace (1920) estimated that normal corn yields were obtained with average temperatures of 70° to 71°F. At cooler temperatures yields were below normal. Maximum yields were obtained at temperatures of 72° to

73°F., with temperatures of 76°F. or above giving a decrease in yields. Normal yields were obtained with 2.5 inches of rainfall in August, with smaller amounts giving decreased yields and greater amounts giving increased yields.

August rainfall showed a positive correlation with yield in almost all areas, although in the center of the Corn Belt the correlations were low. Correlations were especially high in the southwest section. For low amounts of rainfall in Indiana, Hendricks and Scholl (1943) found higher August temperatures gave decreased yields. For higher amounts of rainfall in Indiana and for all amounts in Ohio and Iowa, increased temperatures gave increased yields. This positive relationship may have been due to their considering temperature and rainfall jointly. For temperatures above about 70°F. they found large increases in yield for Iowa and Illinois but only small increases for Indiana (see Tables I and II).

e. September. By September the corn crop is well along and may well be carried to maturity by soil moisture reserves. If none are available, further dry weather may cause a decrease in yield, especially if accompanied by high temperatures. An early freeze occurring in September before the maximum dry weight is reached may cause a serious reduction in yield, especially if the crop is late.

2. Seasonal

Total seasonal rainfall has generally not given high relationships with yield. Pengra (1946) found that seasonal precipitation in the northern Great Plains was more highly correlated with corn yields ($r = 0.58$) than was preseasonal precipitation. A combination of both seasonal and preseasonal precipitation improved this very little. Davis and Palleson (1940) found that at Wooster, Ohio, total seasonal rainfall was not correlated with yields, but the distribution of seasonal rainfall was. Kiesselbach (1950) found that the total of June, July, and August precipitation in Nebraska was significantly correlated with yield, as was annual precipitation, October 1 to September 30.

The effect of precipitation on final yield depends not only upon the amount and distribution of precipitation but also upon the particular combination of other weather factors that happen to be associated with precipitation at that time.

Hendricks and Scholl (1943) measured the effects of different amounts of precipitation at different temperatures using weekly intervals. For Ohio the greatest effect of precipitation for temperatures of 80° to 90°F. occurred just prior to the middle of July, for Indiana in late June, and for Iowa about the middle of June. At temperatures of

70°F., the greatest effect of an inch of precipitation for Indiana occurred about the middle of July. On the basis of many correlation and weather studies the effectiveness of precipitation in June is indeed surprising, although it is a period of very rapid vegetative growth. It is not the time when dry weather is often encountered. That is the time we think of precipitation as, at least, being most necessary.

In Nebraska, Kiesselbach (1915) found that for each rise of 1°F. in mean seasonal temperature during June, July, and August there was a 6.75 bushel decrease in yield per acre. In other less dry areas, this would not be expected to hold, at least to such an extreme degree. A 1-inch increase in July, seasonal, and annual (crop year) rainfall resulted in yield increases of 5.15, 3.32, and 2.08 bushels per acre, respectively. For given amounts of precipitation, except for very small amounts, the greatest effectiveness of temperature found for Ohio was early July, for Indiana late June, and for Iowa late May. In combining the three most important monthly weather factors Wallace (1920) used May and July temperature and August rainfall for Iowa. According to the stage of development of the corn plant these would correspond to temperatures during early growth near planting time and during rapid vegetative growth from approximately knee high to silking, and precipitation near the time of pollination, fertilization, and early grain production.

The effectiveness of rainfall or temperature alone in explaining yield variations depends upon the area being studied. Davis and Harrell (1941) found that the rainfall regression formula alone accounted for a portion of the total variance in yield, ranging from 22 per cent at Wooster, Ohio, to 66 per cent at Manhattan, Kansas, and that the temperature regression formula alone accounted for from 24 per cent of the variation in Pennsylvania to 81 per cent in Manhattan.

Another approach with respect to rainfall was taken by Barger and Thom (1949a). They determined the minimum amount of n -week rainfall, i.e., the amount of rainfall for any length period from 1 to 16 weeks, that would just permit normal corn development. They found that this amount increased parabolically with duration and differed considerably among Iowa weather stations. The drought thresholds for different Iowa stations are given in Table III. If the rainfall for any length period falls below the amount given, a drought is said to exist. No attempt was made to evaluate the influence of temperature and humidity conditions or any other factor directly except rainfall. Correlations between maximum rainfall deficits during the growing season and deviations of county corn yields from normal show that, for years in which drought conditions occurred, from 25 to 60 per cent of the total varia-

tion in yield was explained by this criterion. They (1949b) found what appear to be distinct differences in drought hazard at various locations in Iowa. For example, although southern Iowa enjoys a rainfall probability comparing favorably with other areas in the state, the rainfall requirements are so high that drought is much more likely to occur.

TABLE III
DROUGHT BASE AMOUNTS IN INCHES AT VARIOUS STATIONS AS DETERMINED BY
REGRESSION
(Barger and Thom, 1949b)

<i>Duration</i> <i>n (weeks)</i>	<i>Station</i> <i>(section of Iowa)</i>				
	<i>Rock Rapids</i> <i>(nw)</i>	<i>Fayette</i> <i>(ne)</i>	<i>Ames</i> <i>(c)</i>	<i>Clarinda</i> <i>(sw)</i>	<i>Fairfield</i> <i>(se)</i>
1.	— ^a	—	—	—	—
2.	—	0.13	— ^a	0.19	—
3.	0.30	0.42	0.32	0.68	0.43
4.	0.74	0.80	0.71	1.20	0.96
5.	1.22	1.28	1.14	1.74	1.55
6.	1.72	1.85	1.61	2.30	2.21
7.	2.26	2.52	2.13	2.89	2.92
8.	2.83	3.28	2.68	3.50	3.71
9.	3.43	4.15	3.27	4.13	4.55
10.	4.07	5.10	3.90	4.79	5.45
11.	4.73	6.15	4.58	5.48	6.42
12.	5.43	7.30	5.29	6.17	7.45
13.	6.16	8.54	6.05	6.92	8.55
14.	6.93	9.88	6.84	7.67	9.70
15.	7.72	11.32	7.68	8.45	10.92
16.	8.55	12.85	8.56	9.26	12.20

^a Negative amounts from regression omitted.

Soil characteristics and evaporation conditions were suggested as the possible explanation for the greater needs in certain areas.

Pettis (1951) used a somewhat arbitrary method of determining reduction in corn yields, but the approach used is of interest. This so-called “dry days” method of approach, although somewhat arbitrary, may provide a means of estimating corn yield. For the first 30 days of growth he found that the corn needed relatively little water, 0.2 inch the first week, 0.3 inch the second week, 0.4 inch the third week, and 0.5 inch the fourth week. After this, for the next 60 days the need was

considered to be 0.1 inch per day. The amount of runoff from heavy rains was considered by reducing the number of days these rains were effective. Where a 1-inch rain supplied moisture for 10 days, a 1.5-inch rain supplied moisture for only 13 days, and all rains above 3 inches supplied moisture for 17 days. Unless further rains occurred, dry days were present and a dry day decreased the yield 1 bushel. Further corrections were made for wet-weather damage, but he did not consider temperature or humidity factors. In carrying out his method further one could suggest including temperature data to determine hot and cold days detrimental to the corn, and in addition varying the water consumption for these days and for different stages. This needs to be related to the amount of moisture the soil will hold and the amount of area from which the roots will absorb water. However such a procedure may rapidly become too complex for practical use.

3. Stage of Crop Development

It is known that the plant responds differently to weather factors during different stages of development, but most of the work on yield prediction has considered this fact very little. The crop is at a certain stage of development on different calendar dates in different years, and for this reason calendar dates may average over different stages of development.

J. Warren Smith (1914) realized this and used phenological data collected on corn in Ohio to compute the correlation coefficients given in Table IV. He found the 10-day period after blossoming to be the most critical of those studied with regard to rainfall. If calendar dates were used, he found the 10-day period from July 11 to 20 to be the most

TABLE IV
RESULTS OF CORRELATION BETWEEN RAINFALL AMOUNTS AND CORN YIELD,
WAUSEON, OHIO, 1883-1912
(Data of J. Warren Smith)

<i>Correlation factors</i>	<i>Correlation coefficient</i>
Rainfall for 10 days before planting and yield of corn	0.01
Rainfall from date of planting to date above ground and yield	0.06
Rainfall from date above ground to date of blossoming and yield	0.03
Rainfall from date of blossoming to date ripe and yield	0.29
Rainfall from 5 days before blossoming to 5 days after blossoming and yield	0.45
Rainfall for 10 days before blossoming and yield	0.20
Rainfall for 10 days after blossoming and yield	0.74
Rainfall for 20 days after blossoming and yield	0.57
Rainfall for 30 days after blossoming and yield	0.46

important or for a 30-day period it was from the middle of July to the middle of August, a period which normally includes blossoming. The work of Wallace and Bressman (1937) in southern Iowa, Miller and Duley (1925) in Missouri, Robb (1934) in Kansas, Davis and Pallesen (1940) in Ohio, and Houseman and Davis (1942) in western Iowa all show the period around tasseling and silking to be the most important. During the period of rapid vegetative growth, rain might also be expected to be of great importance. Dale (1948) found a double peak of rainfall effectiveness: one peak from about three to six weeks prior to silking and the second in the period beginning at the date of 75 per cent silking. The first would correspond fairly well with the early part of the period of maximum vegetative growth, and the second corresponds to the period of rapid ear growth.

4. Ideal Corn Season

It is logical to assume that corn yield in the heart of the Corn Belt is somewhat affected by the factors significant on the surrounding margins, but with several factors operating together, generally somewhere near their optima, variation of any one factor may have little effect by itself unless the variation is extremely large. Correlation studies indicate that small deviations in weather factors appear to have little effect on yield in these areas. In the marginal or border areas, certain factors are definitely limiting, and any change in these factors registers as a change in yield. In the west and southwest it appears that high temperatures from midseason on, especially when rainfall is low, are the prime factors in reducing yield. In the south section, factors are not as limiting, but temperatures appear to be too high after midseason. In the north early-season temperatures are too cool, and, coupled with a shorter growing season, limit yields in that area. In the eastern part early-season temperatures may be too cool.

For an ideal corn season in the central part of the Corn Belt (Wallace and Bressman, 1937) the following are desired.

May—mean temperature 65°F. (warmer than average), 3.5 inches of rain (less than normal).

June—mean temperature 71°F. (slightly warmer than normal), 3.5 inches of rain (less than normal).

July—mean temperature 73°F. (cooler than average), 4.5 inches of rain (greater than normal).

August—mean temperature 73°F. (near normal), 4.5 inches of rain (greater than normal).

September—warmer and drier than average, especially if the earlier months have been cool.

The highest average state yields obtained in Iowa were in 1948 (60.5 bushels per acre) and 1952 (62.2 bushels per acre). The average state weather conditions were as follows:

<i>Month</i>	<i>1948</i>		<i>1952</i>	
	<i>Temp., °F.</i>	<i>Precip. In.</i>	<i>Temp., °F.</i>	<i>Precip. In.</i>
May	59	2.3	60	3.8
June	68	3.4	74	5.4
July	75	4.1	75	3.8
August	74	2.5	70	4.8
September	Warmer and drier than normal		Very dry	

In 1948 the weather was cooler early in the season and drier late in the season than the "ideal temperatures" previously given. The effect of the late dry period was partially counteracted by an ideal rainfall distribution throughout the year. In 1952 June and July were warmer than the "ideal season," but May and August were cooler. Except for July, precipitation was slightly heavier than the proposed ideal season. In both years September had excellent weather for drying and maturing the corn crop.

VI. Other Weather Factors

1. Hail

Hail is an important weather phenomenon in that it can cause serious reduction in yield. Considerable work has been done on measuring this reduction by artificial defoliation (Dungan, 1928; Eldridge, 1935, 1936; and Camery and Weber, 1953).

Total defoliation is more serious at certain stages than at others. If the hail damage is early, the plant will largely recover from even complete defoliation. Total defoliation when the plants were about 40 per cent tasseled resulted in almost total loss. With later defoliation the yields gradually increased because more and more of the crop had been made before the leaves were removed.

Partial defoliation caused less severe injury (Table V). To cause very severe yield losses, defoliation must be over 50 per cent. Shredding of leaves done by whipping with a wire brush removed part of the leaf area, and yield reduction was proportional to leaf area removed. Yield reduction was greatest when injury occurred near the time of tasseling.

2. Wind and Evapotranspiration

In determining the effect of moisture on yield, one of the difficulties encountered is in determining how much water is used by the plant.

Although it is not possible to control soil moisture, except under irrigated conditions, it is of value to know under what conditions maximum yield is obtained. Under varying conditions of soil moisture, Kiesselbach and Montgomery (1910) and Kiesselbach (1915) found that the largest actual ear weight was produced at 60 per cent soil saturation, whereas maximum total plant weight was attained at 80 per cent relative saturation. At higher moisture contents greater plant growth was obtained but not with commensurate ear growth. The least water used per gram of dry weight produced occurred in the range of 45 to 60 per cent soil saturation. Maximum water loss from the potometers occurred from 1 to 4 P.M., with a peak at 2 P.M. Transpiration increased from

TABLE V

YIELDS, AS PER CENT OF CHECK PLOT, FROM CORN SUBJECTED TO SIX LEVELS OF DEFOLIATION AT FOUR STAGES OF GROWTH, AMES, IOWA, 1949-1950
(After Camery and Weber, 1953)

Stage of growth	Per cent defoliation					
	0	10	25	50	75	100
11-12 leaves	100.1	95.6	89.1	74.7	52.1	19.6
40% tassel	101.9	97.3	90.1	73.4	46.7	0
Silks 75% dry	95.8	93.3	89.3	70.6	54.2	20.3
Milk	102.3	100.4	99.5	80.7	69.2	47.8

early morning until that time, then decreased after that time until evening. The average hourly night transpiration amounted to only 7.5 per cent of the hourly day loss.

Kiesselbach (1915) found that weekly water requirement early in the season was low and increased until maximum leaf area was reached around late July. Water consumption in the next four to five weeks accounted for almost one half of the total water consumed by the plant. Seasonal climatic variation also caused marked differences between years in the amount of water lost.

Wind is a very important component when considering water loss. Most empirical equations use it as one of the factors for computing evaporation. Wind velocities in a corn field are greatly retarded from that in the open or above the corn. According to unpublished data of the author the movement in the field may be only a small per cent of that above or outside the field.

Water loss has been found to increase with temperatures, and where it was estimated that an acre of maize, with a transpiring surface of approximately 4 acres, lost 3.5 inches of water in 30 days with a mean

temperature of 70°F., it was estimated it lost over 6 inches at 80°F. (Kiesselbach, 1915).

Lysimeters have been used in studying water consumption of plants. One disadvantage of these is that the plants may be more or less isolated. The surrounding area may be of another type of vegetation and artificial micro-climatic influences may be induced. The horizontal advection of air may cause considerable differences from what might be expected in a large area. Large 0.002 acre lysimeters have been used by Harrold and Dreibelbis (1951) to measure water loss. Average daily

TABLE VI
WATER USE BY CORN CROP BY SEMIMONTHLY PERIODS, 1941, 1945, 1949
(After Harrold and Dreibelbis, 1951)

<i>Month</i>	<i>Water used, in inches</i>			<i>Avg.</i>
	<i>1941</i>	<i>1945</i>	<i>1949</i>	
May 1-15	1.0	2.2	0.8	1.3
May 16-31	2.0	2.1	2.1	2.1
June 1-15	1.5	1.6	1.9	1.7
June 16-30	1.6	1.8	2.7	2.0
July 1-15	2.7	2.3	3.5	2.8
July 16-31	3.0	2.0	3.5	2.8
Aug. 1-15	2.1	2.1	3.2	2.5
Aug. 16-31	1.9	1.6	1.7	1.7
Sept. 1-15	1.3	1.6	1.3	1.4
Sept. 16-30	0.3	1.4	0.8	0.8
<i>Total</i>	17.4	18.9	21.5	
Crop yield, bu./acre	80	34	144	
Pounds of water used per pound of dry crop	394	586	334	

water loss for one lysimeter averaged 0.26 inch per day in July, 1949. This rate is considerably higher than those empirically determined by Pettis (cf. Sec. 5, subsec. 2). It is also higher than the limited data of Suomi (1952), who took measurements over a relatively uniform 40-acre area of corn on eight different days. Although he recorded a maximum hourly loss of 0.025 inch per hour on May 28, the largest total daily loss was slightly less than 0.2 inch, with other days averaging around 0.1 inch. The difference may be in part accounted for by the relatively open location of the lysimeters in reference to the surrounding vegetation. Data taken from the 0.002 acre lysimeters (Harrold and Dreibelbis, 1951) show that the amount of water transpired and evaporated in the production of corn crops, computed on an acre basis, ranged from

17.4 to 24.6 inches for three different years. Depletion of soil water supplies by corn was greatest in July. In late August and September the corn frequently suffered from lack of water and the water loss was reduced. For one lysimeter the water loss by semimonthly periods is given in Table VI. In early spring months appreciable amounts of dew formation were measured, although during the summer months these amounts were diminished.

3. Radiation and Sunshine

The amount of radiation is fundamental in determining the amount of water loss. With increased radiation the water loss would be expected to rise and particularly in drier areas solar radiation is negatively correlated with yields. By means of regression Kiesselbach (1950) found that a seasonal increase in per cent sunshine of 1 per cent reduced the grain yield by 1.53 bu., while an increase of 1 gram calorie in the seasonal mean daily total radiation reduced the yield by 0.42 bu. In areas less dry and hot one might expect this to be reversed, although McCalla, Weir, and Neatby (1939) found a negative correlation between growth and sunlight at Edmonton, Alberta, Canada. Few quantitative data, however, are available on the relationship between solar radiation and corn yield.

4. Humidity

Relative humidity is often used as an expression for the dryness of the atmosphere. Since it is a function of both temperature and moisture in the atmosphere, it does not give the true evaporating power of the atmosphere. However, it can be recorded directly, and because of this is often used in agriculture. It is generally believed that in seasons with low relative humidity the corn may suffer more from lack of water, although the relationship between relative humidity and growth rate may be poor (McCalla, Weir and Neatby, 1939). This is at least partially substantiated by Kiesselbach (1950), who found that an increase of 1 per cent in mean seasonal relative humidity increased the yield on the average of 2.73 bu. per acre.

VII. Concluding Remarks

The preceding review has dealt largely with conditions found in the Corn Belt; even so they present a somewhat inconclusive answer to certain questions. In spite of the fact that weather and its relation to crop yields have been studied for many years, few of the problems or questions involved have been given complete or satisfactory answers. This is because of the complex interaction between meteorologi-

cal factors themselves, and the complex relationship between these components of weather and plant development. It may well be many years before these questions are satisfactorily answered.

REFERENCES

- BAIR, R. A. 1942. Growth rates of maize. *Plant Physiol.* **17**: 619-631.
- BARGER, G. L., and THOM, H. C. S. 1949a. A method for characterizing drought intensity in Iowa. *Agron. J.* **41**: 13-19.
- BARGER, G. L., and THOM, H. C. S. 1949b. Evaluation of drought hazard. *Agron. J.* **41**: 519-526.
- BROWN, E. B., and GARRISON, H. S. 1922. Effect of date of seeding on germination. *U. S. Dept. Agr. Bull.* **1014**.
- CAMERY, M. P., and WEBER, C. R. 1953. Effects of certain components of simulated hail injury on soybeans and corn. *Iowa Agr. Expt. Sta. Research Bull.* **400**.
- DALE, R. F. 1948. Influence of phenological period rainfall on the yield of corn in Iowa. Unpublished M.S. thesis, Iowa State College, Ames, Iowa.
- DAVIS, F. E., and HARRELL, G. D. 1941. Relation of weather and its distribution to corn yields. *U.S. Dept. Agr. Tech. Bull.* **806**.
- DAVIS, F. E., and PALLESEN, J. E. 1940. Effect of the amount and distribution of rainfall and evaporation during the growing season on yields of corn and spring wheat. *J. Agr. Research* **60**: 1-23.
- DECKER, W. L. 1947. Estimation of silking date of corn in Iowa. Unpublished M.S. thesis, Iowa State College, Ames, Iowa.
- DUMENIL, L., and SHAW, R. H. 1952. You can "hasten" corn maturity. *Farm Science* **6**: 162-164.
- DUNGAN, G. H. 1928. Effect of hail injury on the development of the corn plant. *J. Am. Soc. Agron.* **20**: 51-54.
- DUNGAN, G. H. 1944. Yield and bushel weight of corn grain as influenced by time of planting. *J. Am. Soc. Agron.* **36**: 166-170.
- ELDREDGE, J. C. 1935. The effect of injury in imitation of hail damage on the development of the corn plant. *Iowa Agr. Expt. Sta. Research Bull.* **185**.
- ELDREDGE, J. C. 1936. Hail damage to corn. *Iowa Agr. Expt. Sta. Research Bull.* **348**.
- FINCH, V. C., and BAKER, O. E. 1917. "Geography of the World's Agriculture." Government Printing Office, Washington, D.C.
- GOODE, G. P. 1939. "School Atlas," pp. 12-20. Rand McNally & Company, New York.
- HANNA, W. F. 1924. Growth of corn and sunflowers in relation to climatic conditions. *Botan. Gaz.* **78**: 200-214.
- HANNA, W. F. 1925. The nature of the growth rate in plants. *Sci. Agr.* **5**: 133-138.
- HARROLD, L. L., and DREIBELBIS, F. R. 1951. Agricultural hydrology as evaluated by monolith lysimeters. *U.S. Dept. Agr. Tech. Bull.* **1050**.
- HAYNES, J. L. 1948. The effect of availability of soil moisture upon vegetative growth and water use in corn. *J. Am. Soc. Agron.* **40**: 385-395.
- HENDRICKS, W. A., and SCHOLL, J. C. 1943. The joint effects of temperature and precipitation on corn yields. *North Carolina Agr. Expt. Sta. Tech. Bull.* **74**.
- HERSHEY, A. L. 1934. A morphological study of the structure and development of the stem and ears of *Zea Mays* L. Unpublished Ph.D. thesis, Iowa State College, Ames, Iowa.
- HEYNE, E. G., and LAUDE, H. H. 1940. Resistance of corn seedlings to high temperatures in laboratory tests. *J. Am. Soc. Agron.* **32**: 803-814.

- HOLBERT, J. R., and BURLISON, W. L. 1929. Studies of cold resistance and susceptibility in corn. *Phytopathology* **19**: 105-106.
- HOUSEMAN, E. E., and DAVIS, F. E. 1942. Influence of distribution of rainfall and temperature on corn yields in western Iowa. *Iowa Agr. Expt. Sta. Research Bull.* **65**: 533-545.
- HUNTER, J. W., LAUDE, H. H., and BRUNSON, A. M. 1936. A method for studying resistance to drought injury in inbred lines of maize. *J. Am. Soc. Agron.* **28**: 694-698.
- HUTCHESON, T. B., and WOLFE, T. K. 1919. Effect of soil moisture and maturity in maize. *Virginia State Tech. Bull.* **14**: 73-92.
- Iowa State Dept. of Agriculture. 1949. Iowa corn phenology summary. Mimeographed.
- IRWIN, J. O. 1931. On the influence of soil temperature on the germination interval of crops. *J. Agr. Sci.* **21**: 241-250.
- JENKINS, M. T. 1941. Influence of climate and weather on growth of corn. *Yearbook Agr. U.S. Dept. Agr.*, pp. 308-320.
- JOHNS, D. M., and BROWN, H. B. 1941. Effect of date of planting on corn yields, insect infestation and fungous diseases. *Louisiana State Bull.* **327**.
- KIESSELBACH, T. A. 1915. Transpiration as a factor in crop production. *Nebraska Agr. Expt. Sta. Research Bull.* **6**.
- KIESSELBACH, T. A. 1950. Progressive development and seasonal variation of the corn crop. *Nebraska Agr. Expt. Sta. Research Bull.* **166**.
- KIESSELBACH, T. A., and MONTGOMERY, E. G. 1910. The relation of climatic factors to the water used by the corn plant. *Nebraska Agr. Expt. Sta. Annual Rept.* **24**.
- KINCER, J. B. 1919. Temperature influence on planting and harvest dates. *Monthly Weather Rev.* **47**: 312-323.
- KLAGES, H. K. W. 1942. "Ecological Crop Geography." The MacMillan Company, New York.
- KÖPPEN, W. 1931. "Grundriss der Klimakunde." Walter de Gruyter, Berlin.
- LEHENBAUER, P. A. 1914. Growth of maize seedlings in relation to temperature. *Physiol. Researches* **1**: 247-288.
- LOOMIS, W. E. 1934. Daily growth of maize. *Am. J. Botany.* **21**: 1-6.
- LOOMIS, W. E. 1937. The chemical composition of drought-injured corn plants. *J. Am. Soc. Agron.* **29**: 697-702.
- MANGELSDORF, P. C. 1929. Corn varieties in Texas, their regional and seasonal adaptations. *Texas Agr. Expt. Sta. Bull.* **397**.
- MCCALLA, A. G., WEIR, J. R., and NEATBY, K. W. 1939. Effects of temperature and sunlight on the rate of elongation of stems of maize and gladiolus. *Can. J. Research* **C17**: 388-409.
- MILLER, M. F., and DULEY, F. L. 1925. The effect of a varying moisture supply upon the development and composition of the maize plant at different periods of growth. *Missouri Agr. Expt. Sta. Research Bull.* **76**.
- NEWHALL, F. 1947. The influence of temperature on the time interval between planting and emergence of corn in Iowa. M.S. thesis, Iowa State College, Ames, Iowa.
- NEWLIN, J. J. 1948. The role of weather in the growth of corn and seed corn in Polk Co. Iowa. *Bull. Am. Met. Soc.* **29**: 5-8.
- PADDICK, M. E. 1944. Vegetative development of inbred and hybrid maize. *Iowa Agr. Expt. Sta. Research Bull.* **331**.
- PENGRA, R. F. 1946. Correlation analysis of precipitation and crop yield data for the sub-humid areas of the northern Great Plains. *J. Am. Soc. Agron.* **38**: 848-849.

- PETTIS, C. R. 1951. Article by Cunningham, G. Are little 'dry days' the real corn robbers? *Iowa Farm and Home Register*, Dec. 2, pp. 3-54.
- ROBB, A. D. 1934. The critical period of corn in northeastern Kansas. *Monthly Weather Rev.* **62**: 286-289.
- ROSE, J. K. 1936. Corn yield and climate in the Corn Belt. *Geog. Rev.* **26**: 88-102.
- RUSH, G. E., and NEAL, N. P. 1951. The effect of maturity and other factors on stands of corn at low temperatures. *Agron. J.* **43**: 12-116.
- SELLSCHOP, J. P. F., and SALMON, S. C. 1928. The influence of chilling above the freezing point on certain crop plants. *J. Agr. Research* **37**: 315-338.
- SHAW, R. H. 1949. Studies on corn phenology and maturity in Iowa. Unpublished Ph.D. thesis, Iowa State College, Ames, Iowa.
- SHAW, R. H., THOM, H. C. S., and BARGER, G. L. 1954. "The Climate of Iowa." 1. The occurrence of freezing temperatures in spring and fall. *Iowa Agr. Expt. Sta. Special Rept. No. 8*.
- SHAW, R. H., and LOOMIS, W. E. 1950. Bases for the prediction of corn yields. *Plant Physiol.* **25**: 225-244.
- SHAW, R. H., and THOM, H. C. S. 1951a. On the phenology of field corn, the vegetative period. *Agron. J.* **43**: 9-15.
- SHAW, R. H., and THOM, H. C. S. 1951b. On the phenology of field corn, silking to maturity. *Agron. J.* **43**: 541-546.
- SMITH, J. W. 1914. The effect of weather upon the yield of corn. *Monthly Weather Rev.* **42**: 78-93.
- SUOMI, V. E. 1952. Heat budget of University of Wisconsin cornfield. Mimeographed Notes.
- TATUM, L. A. 1940. Cold resistance in maize as detrimental in field and refrigerator tests. M.S. thesis, Iowa State College, Ames, Iowa.
- VERDUIN, J., and LOOMIS, W. E. 1944. Absorption of carbon dioxide by maize. *Plant Physiol.* **19**: 278-293.
- VISHER, S. S. 1940. Weather influences on crop yields. *Econ. Geog.* **16**: 437-443.
- WALLACE, H. A. 1920. Mathematical inquiry into the effect of weather on corn. *Monthly Weather Rev.* **48**: 439-446.
- WALLACE, H. A., and BRESSMAN, E. N. 1937. "Corn and Corn Growing." John Wiley & Sons, New York.
- WARD, R. DEC. 1919. The larger relations of climate and crops in the United States. *Monthly Weather Rev.* **47**: 238-240.
- WOLFE, T. K. 1927. A study of germination, maturity and yield in corn. *Virginia State Tech. Bull.* **30**.

CHAPTER VIII

Corn Culture

G. H. STRINGFIELD

I. Introduction

The topic "Corn Culture" comprises a varied system of farm operations. The system survives and flourishes in spite of prophets who have spelled out its ending, in spite of carelessness and inefficiency in its application, and in spite of a large body of misinformation about it. The system survives and moves forward because so many alert corn farmers have accepted the new knowledge that emerges year by year from experience and research, and because these farmers have learned to adjust to the new necessities and opportunities of a changing agriculture. They are being rewarded by yields that are more than twice the national average.

Since about 1940 corn culture in the United States has been purged of much excess weight by the absence of excess farm labor. It has prospered by the great expansion of adapted corn hybrids, by large supplies of low-cost nitrogen, by the extended use of limestone, by better practices in soil conservation, by improved and expanded mechanization, all of these and other benefits largely growing out of institutional and industrial research (Fig. 1). Agricultural education by schools and colleges, extension services, farm papers, et cetera, has been a necessary link in the process of revising our corn culture.

In this chapter the writer attempts to define corn culture in the United States in terms of current practices and to discuss possibilities for improved practices. The methods that are indorsed are normally profitable if fitted into otherwise efficient systems, but no attempt has been made to present comparative costs and returns. Like so many other enterprises, corn culture is profitable when done with above-average efficiency, and when the market demand is favorable compared with competing products.

In Table I are given relative custom costs of some cultural operations. The costs are based on Iowa suggestions for custom fees published in January, 1952 (Porterfield and Hull, 1952). The suggested fees have been converted from dollars to bushels of corn using the value

of \$1.65 per bushel. That value is given in U. S. Department of Agriculture, Agricultural Statistics (1952) as the average price received by Iowa farmers for corn in 1951. The Iowa figures are based on cost accounting experience. They include interest, housing, taxes, repairs, servicing, fuel, labor (0.73 bu. of corn per hour), and an operating margin of 25 to 50 per cent.



FIG. 1. Modern corn culture is based in part on research in plant nutrition. Good corn plants are being grown in quartz gravel. Nutrients can be added or removed at will.

II. Soil Requirements

A good corn soil takes in water readily with a minimum of surface runoff. It retains a good supply of available moisture without becoming water-logged. After being saturated with water it readmits air readily for roots and soil organisms. It is deep enough for root penetration, well supplied with available nutrients, and neither strongly acid nor strongly alkaline. It is relatively free of harmful factors, such as toxic materials, destructive soil-borne insects, noxious weeds; and of obstructions such as rocks, stumps, gullies, and steep grades that make mechanical tillage impractical.

Natively the dark, deep, loamy, prairie soils from western Indiana to eastern Nebraska are exceptionally well suited to corn. But through good management many other soils ranging in color through greys, browns, reds, and black and ranging in texture from sandy to clay have

TABLE I
RELATIVE COSTS OF SOME CULTURAL OPERATIONS
(After Porterfield and Hull, 1952)

<i>Operation</i>	<i>Unit of work</i>	<i>Suggested range of custom charges in bushels of corn</i>
Plowing: 2-bottom plow	Acre	1.97 to 2.42
3-bottom plow	Acre	1.67 to 2.12
Discing, 10-foot tandem	Acre	0.70 to 0.85
Drag harrow, 20-foot	Acre	0.45 to 0.52
Cultipacking, double gang	Acre	0.61 to 0.76
Drill planting: 2-row	Acre	1.09 to 1.30
4-row	Acre	0.70 to 0.85
Check-row planting: 4-row	Acre	1.03 to 1.21
4-row and fertilizer	Acre	1.21 to 1.45
Weeder, 4-row	Acre	0.45 to 0.55
Rotary hoe, 2-row	Acre	0.70 to 0.85
Cultivating, 2-row	Acre	0.97 to 1.21
4-row	Acre	0.76 to 0.91
Harvesting, 2-row	Acre	3.03 to 3.64
Hauling from field and elevating	Bu.	0.03 to 0.04
Field silage cutter	Acre	4.55 to 5.45
Haul, fill, and pack silage	Ton	0.91 to 1.15
Shell	Bu.	0.02
Grind shelled corn	Bu.	0.07 to 0.08
Grind ear corn	Bu.	0.07 to 0.09
Spray with 2,4-D	Acre	1.58 to 1.91
Cut stalks, rotary cutter	Acre	1.58 to 1.91

been built into corn soils that compete favorably with the best of the prairie lands.

III. First Preparations

1. Protection against Soil Destruction

Protection against soil destruction has its place in good corn culture along with the immediate production of good crops. Soil protection is largely concerned with the water relations. Corn can be grown successfully on many erodible soils by adopting measures which retard the movement of water over the field, which shield the soil from the direct impact of raindrops, and which accelerate the rate of water intake. The

lesser volumes of water movement over fields of mild slope are retarded by contour planting. Knoblauch (1942) reported cornfield soil losses in New Jersey of 3.6 tons per acre for contour planting compared to 24.9 tons for up-and-down-hill planting. Van Doren *et al.* (1950), working with a permeable prairie soil of only 2 per cent slope in Illinois, reported 1.6 times as much soil loss from noncontoured plots of corn and oats as from contoured plots. The actual acre losses from the corn plots were 2.2 tons for contouring, and 3.7 tons for noncontouring.

A sharp increase in soil loss is to be expected as the degree and length of slope are greater. Zingg (1940) found that doubling the degree of slope increased the total soil loss 2.80 times, and doubling the horizontal length of slope increased the total soil loss 3.03 times. In the longitude of Nebraska and western Iowa, where listing is an acceptable method of planting corn, contour listing appears to have advantages over contour surface planting. Schaller and co-workers (1953) working on a silt loam in western Iowa report a five-year average of 30, 11, and 3 tons of soil loss, respectively, for surface planting up and down hill, surface planting on the contour, and contour listing. When lister ridges break, however, gullying is usually worse than with surface planting. But Schaller and co-workers point out the practical significance of contour listing on terraced fields where lengths of slope are short. The danger of gullying is thereby much reduced.

2. *Parallel Strips*

Strict adherence to contour planting often is extremely inconvenient, and valuable patches of land are put out of rotation by it because of correction strips and areas. A profitable cornfield must have acceptable size and shape as well as the other attributes already listed. Parallel strips of uniform width, supplemented by liberal sod waterways in the natural drainage areas, are a practical compromise on many mildly erodible fields. Or, one strip toward the higher side of the field may be laid out on the contour and the remaining strips laid out parallel with it. Each field is a problem in itself demanding local ingenuity and decision.

3. *Terracing*

Terracing is the next alternative if the erodibility of a field is beyond the corrective power of strip cropping and contour planting. Water-diversion ditches may be required too. Nichols and Chambers (1938) have discussed in some detail the general problem of mechanical erosion control.

4. *Drainage*

Drainage and possibly irrigation are other items that may need attention before the soil is prepared for planting. Corn roots will not grow in waterlogged soil. Furthermore, corn that is on waterlogged soil in the spring usually is first to show the effects of summer drought. Internal drainage resulting from good soil structure is best, but drainage ditches or tile may be needed (Thorp and Scofield, 1938; Haswell, 1938).

5. *Deep Tillage*

Deep tillage is sometimes offered as an answer to the drainage problem. We quote an eminent soil scientist on this point. Bradfield (1952) writes:

“Deep tillage may loosen compact horizons and temporarily improve both aeration and drainage, but unless conditions are made favorable for root development of deep-rooted crops the soil will soon return to its compact state. . . . Deep tillage supplemented with deeper applications of lime and fertilizer, deep drainage and the growth of deep-rooted perennial crops in the rotation combined with a good system of soil and water management offers promise of balancing soil and water resources for maximum crop production.”

6. *Soil Structure*

Even with the mechanics of water control provided, the soil is not yet ready for efficient corn production unless it has a water-permeable, nonpuddling structure (Fig. 2). If this quality must be added, the first item is to lime as needed to bring the pH within the range of 6.5 to 7.0. There are certain potential corn soils in areas of low rainfall that are too alkaline, or more frequently, too saline for corn. Judicious use of irrigation water is required in these cases (Scofield, 1938). In most corn areas, however, the simpler problem of having the soil acidity checked, and liming as needed, will make possible the growth of deep-rooted perennial legume-grass mixtures. These, along with animal manures, if available, are first choice for providing the desirable crumb structure. Less effective, but good, are grass-legume mixtures of catch crops such as rye grass with sweet clover or winter vetch.

The contribution of an alfalfa sod cannot be defined merely by its content of perhaps 120 pounds of newly fixed nitrogen. Neither can the value of a ton of farm manure be defined as 10 pounds of nitrogen, 5 pounds of phosphoric acid, and 10 pounds of potash. In dramatic fashion Kiesselbach and Lyness (1952) credit two years of alfalfa, harvested

for hay in a nine-year rotation, with the following consecutive yield increases: corn 16.2, barley 8.4, winter wheat 4.1, corn 13.8, and oats 0.0 bu. To 12 tons of farm manure applied before wheat in a six-year rotation, they credit: wheat 8.6, corn 17.7, oats 13.4, first year corn 8.7, second year corn 6.4, and barley 5.8 bu. These are extreme cases presumably on land that had been continuously grain cropped for a long period.



FIG. 2. A silt loam soil with good structure has a granular appearance after plowing.

7. Cropping System

A cropping system obviously must be established as a framework in which the first preparations for corn will be made. The contribution to the soil of a good cropping system is primarily that it brings about arrangements of soil particles into loose, crumblike aggregates. Between the aggregates are pore spaces. Both water and air readily enter well aggregated soil. Water drains through it, leaving it moist but not waterlogged. It is a most favorable physical environment for plant roots and soil microorganisms.

The total effect of a corn crop is to break down good soil structure (van Bavel and Schaller, 1950). But of what purpose is good structure other than as a contribution to the production of profitable and highly useful crops such as corn? Page and Willard (1946) found that poor physical condition almost completely limited corn growth on heavy lake-bed Ohio soils. They also found that the cropping system is of great importance in controlling soil structure which may change from season to season. They considered a good cropping system to be one in which the soil structure is alternately built up by one crop and torn down by another.

The beneficial effects of deep-rooted legumes such as alfalfa and kudzu where adapted extend throughout the soil profile, down to a depth of 30 inches (Uhland, 1949). Here is biological deep tillage and drainage in operation. The presence of crop residues on the soil surface has been shown by Yoder (1936) and others to have a marked influence in reducing runoff and soil loss and in improving the soil structure under them. Even corn stalks and corn cobs make good mulches. The stalks as soil cover reduced late fall, winter, and early spring erosion by one-half compared with corn stubble in Missouri experiments (Smith *et al.*, 1948). It is quite possible that by growing big corn crops in dense stands, leaving the stalk mulch on the ground, and following less depleting cultural methods (yet to be perfected) corn may be taken out of the soil-destructive category. As pointed out by Smith (1952) corn is not in itself erosive.

8. *Organic Matter*

The water problem is not solved by intake and drainage alone. Large volumes must be retained by the soil but without waterlogging. Soils of intermediate texture, between sand and clay, and well supplied with decomposed organic matter hold available water best. The farmer cannot change his soil texture, but he can incorporate organic matter through the sods and catch crops already referred to. He can use farm manures if available, and he can leave crop residues in the field unburned.

IV. Lime and Fertilizers

It was pointed out in the previous section that corn must remain in the category of soil-destructive crops until less erosive cultural methods are perfected. Good management requires, therefore, that corn be grown in rotation with crops that build soil structure. It is true that corn has been grown continuously for a generation or more on some bottom lands that are recurrently under slow-moving flood water. There is a

reasonable doubt, however, that many of these fields are as good today as they were for the earlier corn crops.

1. Fertilization

The plan for fertilizing corn is properly centered on fertilizing the rotation as a whole plus a "starter" or row fertilizer and perhaps supplemental nitrogen for the corn. There are numerous experiment station and extension bulletins on fertilizing crop rotations. Pertinent and excellent discussions will be found in Bear (1953) and in the United States Department of Agriculture Yearbooks, *Soils and Men* (1937) and *Science and Farming* (1947).

2. Lime Requirement

The lime requirement will have been assessed and met in good rotational fertilization. This applies even as far west as Nebraska (Kiesselbach and Lyness, 1952). A pH as high as 6.5 is desirable; higher than 7.0 is not advantageous for the corn and may be detrimental in some circumstances. Calcium, the essential ingredient of limestone, affects corn directly as a required nutrient but more importantly by its indirect effects through better legumes, more active microbial action, and greater availability of nutrient elements. Where magnesium deficiency appears in corn, the dolomitic limestones will have a somewhat higher value than the high-calcium limestones. Good rotational fertilization assumes further that the nutrient needs of the other crops in the rotation are so generously provided that the corn will have large residues of available nitrates, phosphates, and potash. Corn requires a number of other elements, too, and these needs give rise to additional fertilizer problems on some of the older soils and on sandy soils. For the great bulk of corn soils, however, lime plus the three elements just listed are the most probable needs at present.

3. Nutrient Requirements

The nutrients taken up in the ears, stover, and roots of an acre of corn yielding 100 bushels of air-dry grain have been variously reported. Smith (1952) reports: nitrogen, 160 to 215 pounds; phosphoric acid, 45 to 80 pounds; and potash, 90 to 175 pounds. The riddle arises in evaluating and adjusting the variables so that the nutrients will be in the soil in available forms, in the quantities needed, and in reasonably balanced proportions. Gross unbalance is obviously wasteful and in some situations may be harmful. The primary variable is the dynamic or changing nature of the soil system. It is not like a warehouse where incoming inventories always can be balanced against removals.

4. Nitrogen

Nitrogen is released from the semipermanent organic reserve, if there is one, at the rate of about 2 per cent for each corn crop (Salter *et al.*, 1936). This might amount to 70 to 80 pounds on a fairly good dark soil. The residue of a good legume sod or catch crop should contain another 80 pounds or more. Nonsymbiotic nitrogen-fixing bacteria contribute variable quantities in different soils and seasons. Each ton of average farm manure should contribute about 10 pounds of nitrogen. Even a ton of dry straw or cornstalks will release, sooner or later, about 20 pounds of nitrogen.

But the rates of releases of this nitrogen are not constant from year to year or from place to place. Cellulose-decomposing bacteria require and make temporarily unavailable about 40 pounds of nitrogen for breaking down a ton of straw or cornstalks—20 pounds more than the residues contain. Even mature legume residues may temporarily tie up more nitrogen than they release.

Nitrates are highly mobile in the soil, moving up as it dries and down with gravitational water. Large quantities can be lost in drainage water, especially in lighter soils. Furthermore, the corn roots will take up only from 40 to 60 per cent of the available nitrogen (Truog *et al.*, 1953).

The fact that corn varies from field to field and from season to season in its response to applied nitrogen is just what should be expected. Furthermore, it should be expected that the greater the dependence on natural supplies, the greater the uncertainty of the need for supplementation with fertilizers. Dark soils in the latitude of Pennsylvania and Iowa and northward are in this category. In these areas supplemental nitrogen will nearly always be profitable on sandy or light-colored (low organic) soils (Prince *et al.*, 1941). More will be profitable in the absence of legume residues; more in the absence of farm manure; more for second-year corn; more as top soil has been lost by erosion.

Much of the older experimental work on these better northern soils would indicate that a small amount of nitrogen applied to the row at planting time would be all that is profitable provided excellent management practices preceded the corn crop (Fig. 3). However, Marriot and Jackson (1952) reported a well-replicated Wisconsin experiment following six years of alfalfa-brome grass sod in which unfertilized plots yielded 127 bu. per acre after adjustment to 15 per cent of moisture. Thirty pounds of nitrogen per acre increased the yield to 144 bu., and 30 pounds of nitrogen plus a row application of 150 pounds of 10-10-10 increased the yield to 149 bu. In this experiment the stand was 18,000

plants per acre. And therein probably lies the difference between it and most of the older work. Not all fields are normally well enough watered for stands that high. But too many of the older Corn Belt fertility tests were conducted at stands quite inadequate for accurate evaluation of the better treatments. The need for conducting field fertility experiments at a stand expected to be optimum for the better treatments was pointed out by Stringfield and Thatcher (1947).

No longer is the profitable use of nitrogen limited to the more humid corn areas. Lowrey and Ehlers (1952) have reported efficient returns

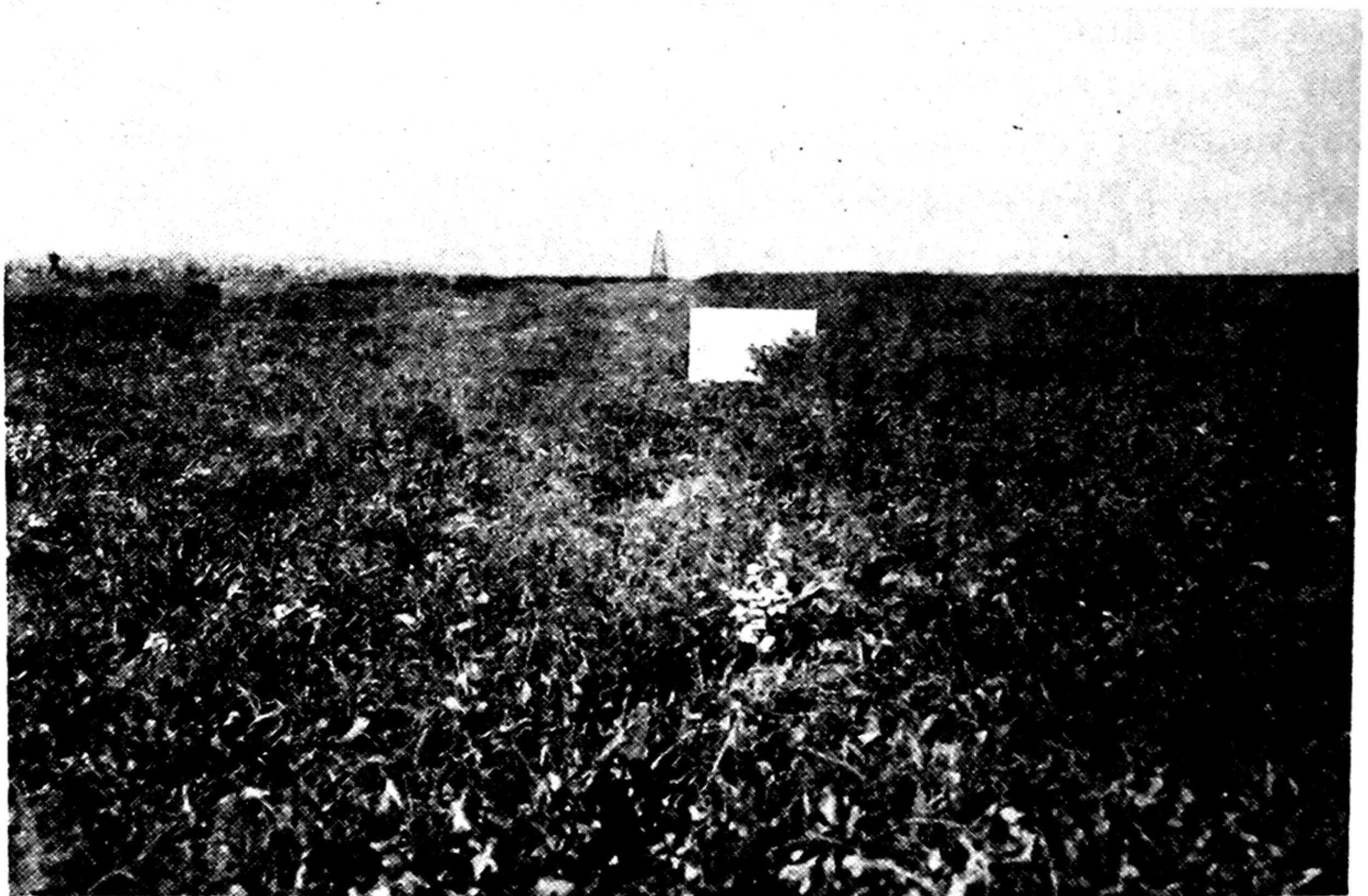


FIG. 3. Supplemental nitrogen almost certainly will be profitable for corn on the Ohio timothy sod at the left. The chances are that it will be profitable following the alfalfa on the right, only for heavy stands of corn and an above-average season. (Courtesy Ohio Agricultural Experiment Station.)

from nitrogen on several eastern Nebraska soils, especially when the corn did not immediately follow a legume. Both irrigated and non irrigated fields were studied. Applying fertilizer to corn in this semihumid area would seem to set the stage for an even greater loss when a dry season comes. But so far as the nitrogen is concerned, the unused portion would be largely available for a crop the following year. It would be unlikely to leach away during the dry year.

As the summer seasons are longer, the leaching of soluble salts and the oxidation of organic matter combine to lower the natural nitrogen content of the soil (Jenny, 1930). The result is that in Missouri supplemental nitrogen on corn is more urgent and its results more

predictable than in Iowa or Minnesota. Likewise, the need and the predictability are greater in Arkansas (Bartholomew, 1948), and North Carolina than in Missouri. Krantz (1949) found in North Carolina that the lowest cost per bushel came with 120 pounds of nitrogen per acre with adequate phosphorus and potash.

This same trend holds in regard to the importance of time of applying nitrogen. On dark soils in the latitude of Ohio ammonia nitrogen for corn may be plowed down with comparative safety during the preceding fall after the soil temperature has dropped to about 50°F. Experiments in this latitude, Pennsylvania to Nebraska, have not uniformly shown a clear advantage for delayed applications of nitrogen as compared with applications at planting time or before (Dumenil, 1952). In North Carolina, however, Krantz (1949) found that the time of applying nitrogen can be almost as important as rate. His work indicated that about one-fourth of the nitrogen should go on at planting time and the remainder when the plants are about 2 to 3 feet high.

Where nitrogen is to be side-dressed, quick action is required, making it essential that the salts or solution be placed in moist soil.

Robertson and Ohlrogge (1952) found little difference whether the nitrogen was placed 10 inches from the row or in the center between the rows. This would seem to suggest the advisability of the center placing because of less danger of root pruning.

Nitrogen can be purchased in more than a dozen forms. The organic forms, cottonseed meal, animal refuse, tobacco by-products, and several others, are now relatively unimportant as fertilizers because of their demand by the feed industry. The more important inorganic forms are sulfate of ammonia, anhydrous and liquid ammonia, nitrate of soda, ammonium nitrate, ammonium phosphate, calcium nitrate, and nitrate of potash (McVikar, 1952). The nitrate forms are immediately soluble in moist soil and subject to leaching. Ammonia is changed to nitrate quickly in moist soil at 57°F. or warmer, but will remain insoluble for long periods at lower temperatures. The liquid forms are usually lowest in price, but they require special equipment for application. Aside from these considerations the choice of nitrogen carriers for corn should be based on cost per unit of nitrogen, including the relative cost of application.

Nitrogen has been given the lion's share of this discussion of corn fertilizers, but only because we are now in the process of learning to use it more liberally. The advent of corn hybrids, their adaptability to heavier stands, and new developments in the commercial synthesis of nitrogen compounds have all contributed to this circumstance. Nitrogen is really no more important than any other of the essential elements.

Each is necessary for efficient utilization of the others. In some future discussion of corn fertilizers, magnesium, or sulfur, or manganese, or some of the rarer elements could have the prominent place.

5. *Phosphorus and Potassium*

Phosphorus and potassium in greater quantities must accompany the current larger use of nitrogen. Neither phosphorus nor potassium can be fixed from the atmosphere; they must be released from slowly decomposing soil minerals or applied. Represented among the Ohio soils are: lacustrine, residual sandstone and shale, residual limestone, glaciated, and nonglaciated. The Ohio Experiment Station (1951) reports that these soils have released to crop plants annually the equivalents of from 7 to 30 pounds of P_2O_5 (phosphoric acid) and from 40 to over 100 pounds of K_2O (potash). It is obvious that both nutrients must be either accumulated or added, or both, before the requirements of 100-bu. corn yields are met. They can be accumulated in part by returning crop residues and animal manures to the soil. Their uptake can be increased in quantity if good stands are attained and if soil conditions are otherwise favorable for deep-rooting and vigorously growing crops.

A favorable balance of phosphorus is the more difficult to maintain, not only because it is released in smaller quantities, but also because it is moved away from the land in grain and bone in greater quantities. Part of the phosphorus is met in some regions from heavy applications of ground rock phosphate. The heavy drain will be on potash if a large volume of legume hay, especially alfalfa, is sold from the farm.

In good cropping systems over wide corn-growing areas the phosphorus and potassium needs for large corn crops are efficiently supplemented with row applications of fertilizer analyses such as 3-18-9 or 0-20-10 at rates of 250 to 300 pounds per acre. A 3-12-12 at the same rate or 0-20-20 at up to 200 pounds usually would be preferred where potash removal from the farm is heavy. Heavier row applications may become safe as more efficient distributing equipment is developed. The row fertilizer should be placed in bands $1\frac{1}{2}$ to 2 inches to the side and 1 to 2 inches deeper than the seed. If closer, the soluble salts, especially potash, may reduce the stand and delay early growth.

How can a corn grower arrive at an efficient fertilizer program?

He can study his growing plants for deficiency symptoms. Corn with yellowish green leaves usually needs nitrogen. This symptom often appears early enough for a beneficial delayed application. If there is a yellowing and dying along the leaf midribs in widening bands toward the tips, the nitrogen deficiency is getting serious. Early dying along

the leaf edges toward the tips suggests potash deficiency (Fig. 4). Purpling, usually accompanied by a lagging growth rate, suggests phosphorus deficiency. All the upper leaves and most of the lower leaves on a healthy well-nourished corn plant will remain green until the crop is nearly mature.



FIG. 4. This corn is suffering from potash deficiency as shown by the dead leaf margins. It suffers also from careless deep cultivation.

Soil scientists are rapidly refining the difficult techniques for testing soils as a basis for fertilizer recommendations. The results of these tests along with a knowledge of the soil type and of the recent field history enable the competent agronomist to make sound recommendations.

V. Final Preparations and Planting

Final preparations for the corn crop begin after the field site has been selected; the field layout has been planned; needed mechanical measures for water control have been taken; the cropping system has

been planned and perhaps begun with structure-building crops; and the fertilizer program has been planned and possibly begun with advance treatments.

1. Seedbed Preparation

A good bed for seeds and seedlings and expanding root systems must be prepared. Farmers call it a seedbed. The objectives are: (1) to put the surface soil in such a condition that the seed can be placed in intimate contact with moist soil and covered for protection against drying and against birds and rodents; (2) to loosen and fluff the soil for temporary improvement of air and water relations, and indirectly to stimulate microbial activity and the release of plant nutrients; and (3) to make ready for easy and efficient planting and cultivation. Covering trashy residues is an objective to the extent that the coverage is necessary for good planting and later tillage. Otherwise some trash on the surface is desirable for better water infiltration and in some locations for the reduction of wind erosion.

The physical condition of a good seedbed obviously is delicate. It can be, and often is, harmed or spoiled by excessive smoothing and "fitting" operations which leave the surface overfine and structureless, or a packed structureless layer may form at disc-depth or from the surface downward under the wheels of heavy machinery. The injury from packing is greater as the soil is in poorer physical condition and as its moisture content is greater. A torrential rain may ruin a seedbed especially on finer textured, low organic soils that are not well aggregated. A good seedbed is more than just a place where seeds sprout. In it the seedling must find easy penetration upward to and through the surface, downward to the subsoil, and horizontally.

The moldboard turning plow is still the preferred implement for loosening and fluffing the soil and disposing of surface trash on reasonably level land roughly east of the 30-inch rainfall line. There is, however, a great overlapping of plowing with listing and other systems in western Iowa and eastern Nebraska.

Surely no tillage operation is quite so demanding of the farmer's good judgment as plowing. Should he plow in the fall? Yes, if winter erosion is no serious hazard, if he has a fine-textured soil that becomes mellow with freezing and thawing, if local experience confirms its value. Some clays must be fall plowed, and fall plowing sometimes has value in insect control. Some silty soils will settle during the winter to their original compactness if fall plowed. The distribution of labor and the cropping system will often influence the rightness of the choice.

Plowing overwet soil usually is very bad. The soil aggregates that

constitute good structure are relatively water stable if left in place, but they have low resistance to pressure when wet—hence the big hard clods that so often follow wet plowing. The soil is too wet for plowing if the furrows turn up slick and shiny and fail to crumble from their own weight, or if a handful of upturned earth can be molded into a ball that sticks together.

Plowing is deep enough if the furrows lie on edge at about a 45-degree angle and a satisfactory covering of surface material is attained. A furrow depth of half to six-tenths its width generally is considered about right for these objectives (Gray, 1938). Deeper plowing adds heavily to the cost, but nothing to the yield of the corn crop. According to Slipper and Silver (1951) high plow speeds, excepting perhaps in sand and muck, are more harmful to soil structure than any other fault in modern plowing. These authors recommend as an ideal that plant residues be evenly sandwiched between the furrow slices from the plow sole to the pit of the V between the furrow crowns.

Smoothing and “fitting” the plowed soil for planting usually is accomplished with combinations of the disc, spike-tooth harrow, cultipacker, spring-tooth harrow, rotary hoe. If early drying of the soil permits plowing well in advance of planting time, a harrowing or light discing immediately after plowing time usually is desirable. It is necessary on soil that will dry into large hard lumps. As planting time approaches the surface will have settled and surface weed seeds will have sprouted. A light discing will loosen the surface and kill the seedlings of annual weeds. Deep discing brings to the surface a new crop of weed seeds, many of which otherwise would have lain dormant for the year. Too much discing destroys structure beneath the surface, and the accompanying tractor wheels do the same at the surface. The spring-tooth harrow is low in compaction and is good if it does not dig up too much trash. The cultipacker breaks soft clods, compacts and fines the surface, kills few weeds. The cultimulcher, a combination spring-tooth harrow and cultipacker, is a good “fitting” tool. Cook and Peikert (1950) have accomplished once-over tillage by attaching to a two-bottom plow a cultimulcher a little wider than the two furrow slices. A narrow section of a rotary hoe, called a tiller, is being used in the same way (Shedd *et al.*, 1942). These tools will reduce expensive and soil-compacting fitting operations on many soils.

Machines that chop the soil with high-speed metal knives or hammers are highly destructive of soil structure.

Mulch tillage, also called trash mulching, stubble mulching, and subsurface tillage, is done with heavy V-shaped blades or small sweeps of heavy field cultivators drawn a few inches under the soil surface.

They lift and loosen the soil but do not turn it. The one-way disc plow, often followed by a rod weeder, is also a mulch-tilling implement. Most of the surface residues are left above ground. The advantage of mulch tillage for corn is limited to porous soil, sloping land, and areas of low rainfall where moisture shortage and erosion by water or wind are extremely hazardous. It is highly effective in conserving water, protecting the soil structure, and reducing erosion. Special furrow openers have been devised for planting through the residues (Duley and Russel, 1939; Borst and Woodburn, 1942). The residues on the surface make effective cultivation difficult. But the most serious objection to mulch culture in the better corn-producing areas is that it fails to produce corn yields that compare favorably with tillage methods based on the turning plow. If and when that defect is eliminated, some modification of mulch culture has a good chance of wide adoption in the humid regions (Norton *et al.*, 1944).

Manure mulching offers some of the advantages of mulch tillage, and some of the disadvantages, but without loss in yield (Borst and Volk, 1952). Six to eight tons of manure per acre are applied to the corn with a manure spreader after emergence and after early weed growth has been controlled. Manure as mulch has increased corn yields as much as the same amount plowed under, and the mulch has conserved an average of 2 inches of rainfall and reduced soil-erosion losses from an average of 15 tons per acre to less than 1 ton on short slopes of erodible soil. Objections are that the soil is left exposed to erosion for a short but hazardous period, that the manure must be applied at a normally busy time, and that cultivation through the mulch is rather unsatisfactory.

2. *Methods of Planting*

The corn planter is used for planting on ground that has been smoothed after plowing or discing or both, that is, surface planting. The essential mechanisms of the corn planter are (1) a plate that revolves at the bottom of a hopper sorting the seed and dropping it into a boot which leads downward to (2) a flat planting shoe which places the seed at the desired depth and allows the soil to fall back over it. A wheel with a concave rim open at the center runs over the planted row firming the soil about the seed. Most modern planters have fertilizer attachments for row or hill application. The requirements for obtaining the desired planting rate are (1) reasonably well-graded seed, (2) the right planter plate for the seed, and (3) moderate driving speeds.

Planting in tractor-wheel furrows on freshly plowed ground can be done by adjusting the rear tractor wheels so that their spacing is the

same as that of the planter shoes. The planter is pulled behind the tractor and the planting is in the firmed and smoothed tractor-wheel furrows. The loose soil between the furrows is relatively unfavorable for quick germination of weed seeds and favorable for water intake. Soil compaction is held to a minimum. The scheme requires (1) a good job of plowing, and (2) a soil that crumbles into a smooth plowed surface and that is made firm but not over packed by the tractor wheels. If the plowed surface is more than moderately lumpy, a smoothing implement either in tandem hitch on the plow or in a separate operation will need to be used between plowing and planting.

Listing has the advantage of preparing the seedbed and planting in one operation. It may be preceded, however, by shredding surface residues, by disking, by blank listing, or by plowing, depending upon the amount and nature of the residues, the hardness of the ground, the possibility of impounding moisture in the blank-listed furrows, or the soddiness of the field. The lister is a combination of (1) a double mold-board plow which throws the soil both left and right, leaving a V-shaped furrow, and (2) a planter, with or without fertilizer attachment, which plants the seed in the bottom of the furrow.

The time saved by listing, over plowing and surface planting, often results in more timely planting of the crop as a whole. Seedbeds are not over packed. Weed control is easy and effective. Small weeds are covered by rolling soil into the furrows with cultivator discs and shovels. Listing offers an opportunity to conserve moisture and reduce erosion (Schaller, 1951).

But germination and seedling growth are slow and poor stands are more frequent in the cold furrow bottoms compared with surface planting (Jenkins, 1934). It is apparently because of the slow start that lister planting is inferior to surface planting throughout most of the better corn-producing areas. Moving west through the central Corn Belt, listing begins to appear on some of the better drained soils in western Iowa and eastern Nebraska. Listing or planting in furrows which are opened in plowed ground appears also to have advantages on some of the more droughty southern soils.

Bedding is the opposite of listing, since the corn is planted on elevated ridges or beds with water furrows between. It is done on some of the more poorly drained southern soils.

3. Time of Planting

The time of planting for the main dent corn crop in the United States begins late in January in the extreme South and moves northward at an average rate of about 13 miles a day, ending in early June

in the extreme North. The normal planting time is well known by farmers in all localities. It usually begins a few days after the average date of the last killing frost, being earlier in warm dry weather and later in cold wet weather. The daytime temperature of the soil where the seed is to be placed should be 60°F. or higher. If good germination and weed control are achieved, relatively early planting usually will have advantages over late. In a 20-year experiment at Wooster, Ohio, the optimum planting time was during the week following May 7. Delays of one, two, and three weeks resulted in losses of 2, 7, and 14 bu. per acre, respectively.

Planting date is perhaps less critical south of the Ohio latitude. Johns and Brown (1941) in Louisiana found no significant difference in yields from planting dates ranging from February 25 to May 15, but found lower yields and increasing injury by insects and diseases when the planting was after May 15. Texas experiments have shown, however, that most varieties drop sharply in yield as planting is delayed after the earlier dates (Manglesdorf, 1929). Georgia tests indicate that medium to early plantings yield best, that late plantings often fail entirely, and that insect damage is usually worse following late planting (Stacy, 1941).

Manglesdorf (1929) showed that within the normal Texas planting period a delay of a day in planting was associated with a delay of half a day in the silking period. Practically the same relation has been observed in northern states.

4. Depth of Planting

The depth of planting is properly regulated by the requirements for placing the seed in intimate contact with warm moist soil and protecting it against rodents, birds, and drying. One inch under settled soil is shallow; 3 inches is deep. The soil dries and warms from the top down. It follows that the location of warm moist soil tends to move downward, requiring deeper planting as the planting season progresses. The seedling develops an underground internode of variable length between the seed and the permanent crown of roots. The depth of the crown is determined by the moisture and air conditions of the soil, not by the depth of the seed. The final depth of the root system is controlled by the heredity and the total environment, rather than by planting depth.

5. Rate of Planting

Rate of planting is of major importance. Adapted hybrids and heavy nitrogen application, two relatively recent developments, have combined to nullify the older recommendations concerning it. Stringfield

and Thatcher (1947) found that optimum stands for adapted hybrids averaged higher than for open-pollinated varieties by about 2000 plants per acre. Heavy nitrogen application, along with adequate phosphorus and potassium, has demanded further increases in plant populations for most profitable returns (Rounds *et al.*, 1951, in Michigan; Jordan, 1951, in Mississippi; Krantz, 1949, in North Carolina; Pendleton *et al.*, 1952, in Illinois; and others).

Optimum stands are higher in the northern states where plants are smaller, and higher where water supply, nutrient supply, and soil

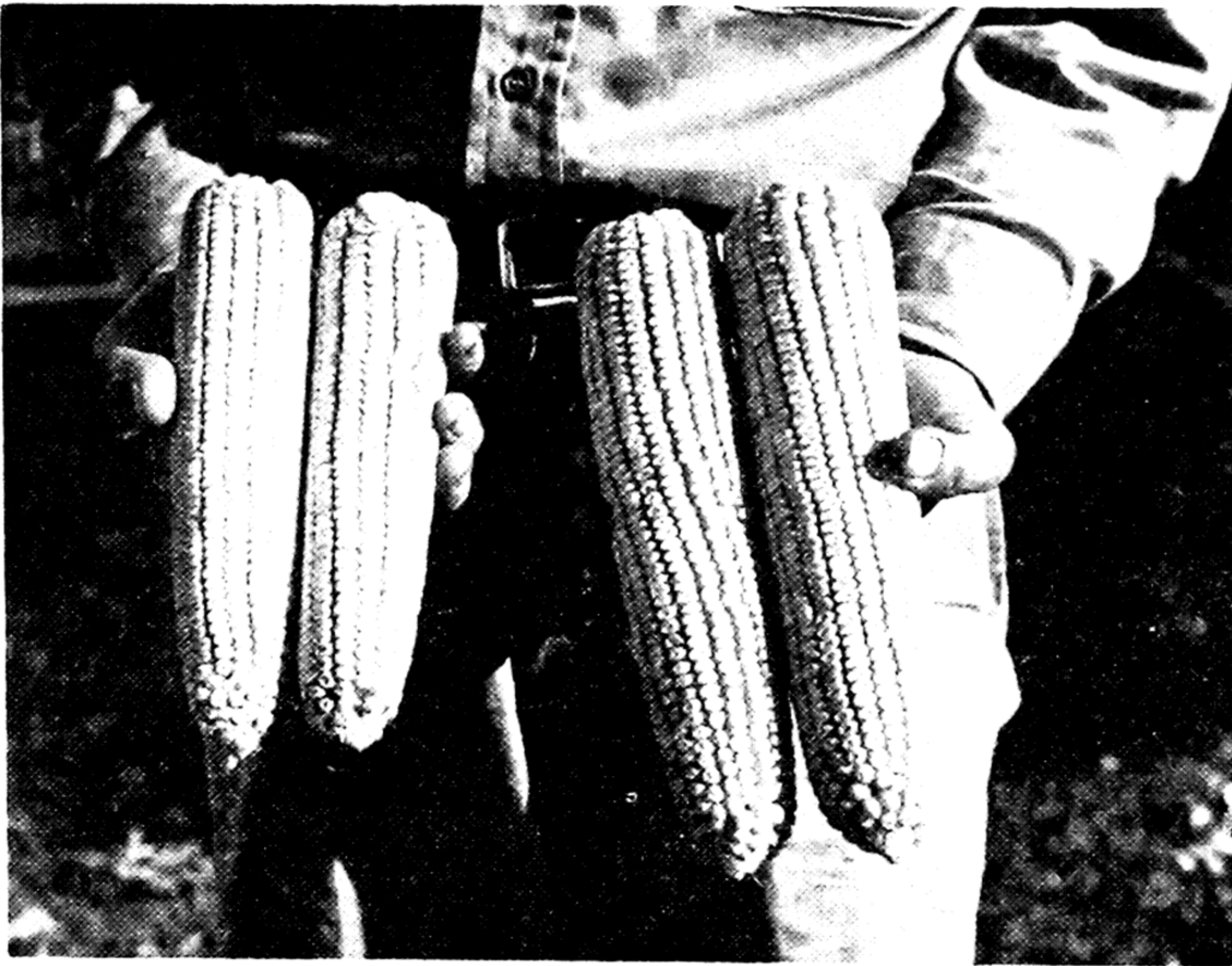


FIG. 5. The $\frac{1}{2}$ -pound ears at the left indicate that the stand was about right for the productivity of the soil. The $\frac{3}{4}$ -pound ears at the right indicate that the stand was too thin by perhaps 5000 plants per acre.

condition are more favorable. Evidence is accumulating that hybrids may have different inherent tolerances of heavy stands quite apart from the variables just listed (Rounds *et al.*, 1951; Pendleton *et al.*, 1952).

From central Indiana eastward recommendations of stand will average about as follows: plan for 9000, 12,000, and 16,000 plants per acre, when anticipated yields are 60 or less, 80, and 100 bu. per acre, respectively; or, if rows are about 42 inches apart, plant one seed in 42 inches of row space for each 20 to 25 bu. per acre of anticipated yield. Stands of 18,000 plants or more per acre are still in the experimental stage where irrigation is not available. The final stand seldom is more than 85 per cent of seeds planted.

In the northern tier of states the optimum stands are heavier than

for the central Indiana latitude, and the optimum stands become lower toward the South and toward the Great Plains. In eastern Texas the recommended rates range from 6500 to 9500 plants per acre (Rogers and Collier, 1952). But whether in Texas, Iowa, Indiana, Ohio, or Pennsylvania, recent investigations indicate that the stand is about right for capitalizing on the productivity of the soil, including water, when the plants average between 0.5 and 0.6 pound of air-dry ear weight (Fig. 5). A tenth of a pound should be added for the southern prolific hybrids.

Minor fluctuations in the distribution of plants are of relatively little importance. Kiesselbach *et al.* (1935) got the same yields whether plants were uniformly in 3-plant hills, or in alternating hills of 2 and 4, or of 1, 3, and 5, or of 1, 2, 3, 4, and 5 plants. As would be anticipated from these results, no clear difference in yield has been established between check-rowing, drilling, or hill dropping. This is in spite of the fact that the incidence of tillering may be several fold higher on singly spaced plants than on plants in hills (Stringfield and Thatcher, 1947). Mechanical weed control is more effective in check-rowed planting, and hills are more resistant to root lodging than are singly spaced plants. Since check-rowing is losing favor under the modern demand for speed, the practice of hill dropping without check-rowing appears sound (Miles, 1951).

VI. Intercropping

Intercropping in corn is as old as the known history of the crop itself. At least some of the American Indian tribes spaced corn hills 4 feet apart or more and interplanted beans or other crops. In parts of the South the practice of planting peanuts and other legumes between widely spaced corn rows is of long standing. Soybeans sometimes are drilled in the corn rows with the hope of obtaining a more nutritive silage crop. The plan of alternating two rows of soybeans with two rows of corn, both to be harvested as grain, is being investigated. But interplantings of legumes or cereal crops that mature with the corn appear to be losing in favor.

1. Corn as a Nurse Crop

The situation is different, however, where the interplanting is of a crop that is expected to survive the corn and to make an important part of its growth after the corn is mature. Cases in point are winter cereals, plow-down crops, and meadow crops. The cultural problems of such intercrops concern the intercrops themselves rather than the corn and will not be discussed in detail here. But the culture of the corn requires modifications to permit successful intercropping.

Successful intercropping with summer-seeded crops demands some sacrifice of corn yields because (1) the intercrop competes with the corn, and (2) the corn must be thinner or the row spaces must be wider than optimum. The row-space adjustment is the more promising.

According to Stringfield and Thatcher (1951) row spaces may be up to 50 inches without loss of yield if the soil productivity is good enough for a 75-bu. yield at conventional spacing and if the acre stand is commensurate with the productivity. These authors further reported average yield reductions of 4 to 5 bu. per acre where the row spaces

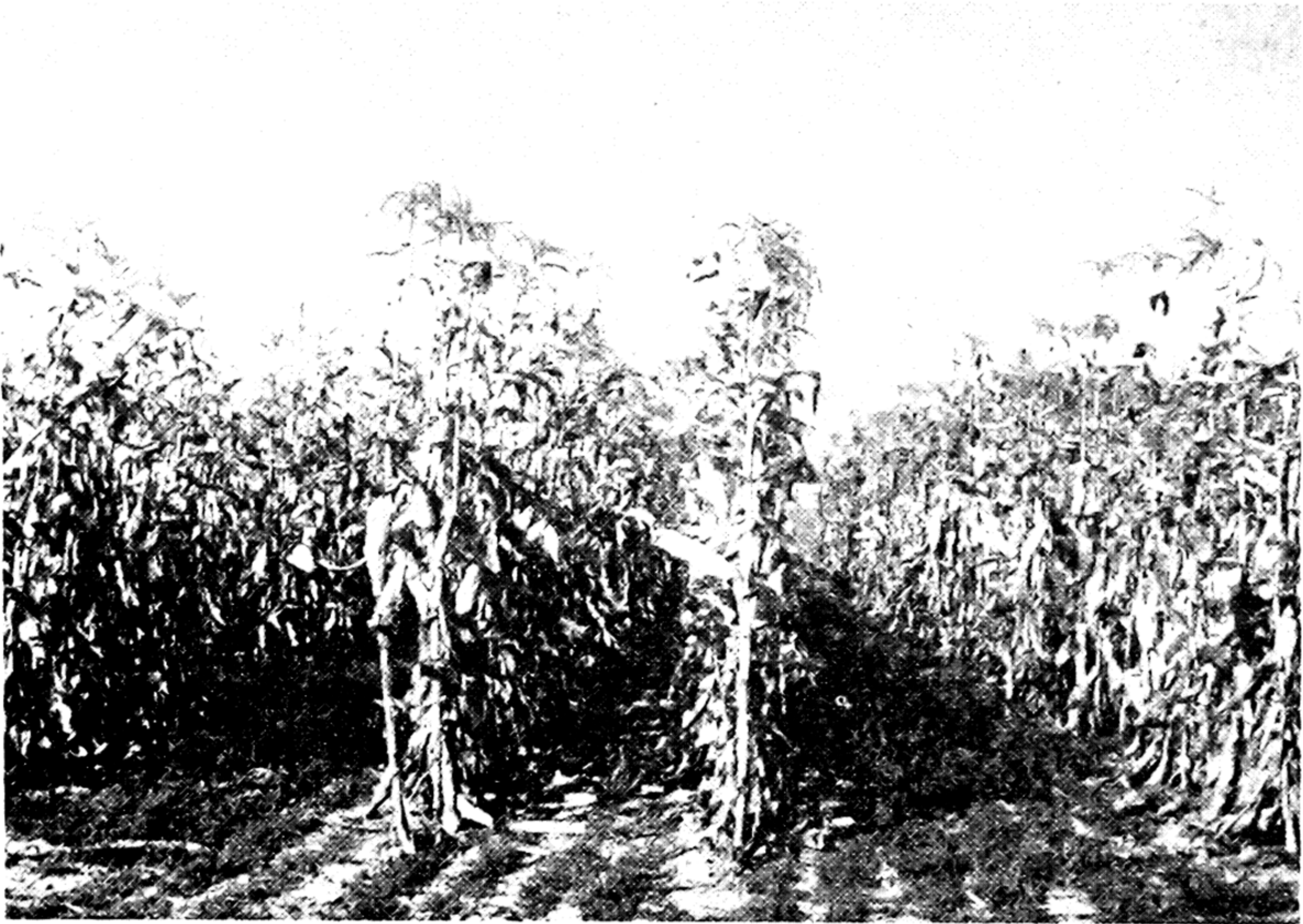


FIG. 6. The corn rows are spaced alternately at 40 and 72 inches. The sweet clover was seeded with a standard grain drill before the corn was knee high.

were 60 inches, and of 9 bu. where row spaces were 70 inches, again on moderately productive soil.

A considerable body of evidence is accumulating which indicates that interplantings in corn of alfalfa, sweet clover, hairy vetch, crimson clover, timothy, domestic rye grass, and other meadow and plow-down crops can be made as successful as other summer seedings. Corn rows should be about 60 inches apart for these crops, or the rows may be alternately 40 and 72 inches more or less. Seedlings can be made with standard grain-drill attachments when the corn is not more than about knee high (Fig. 6). The few bushels of loss in immediate corn yield may be more than compensated by the fact that if corn is a nurse crop it can be grown more often in the rotation.

2. *The Corn-Wheat Sequence*

Corn rows need to be about 72 inches apart to permit running a farm-sized tractor between them for winter wheat seeding. The expected loss in corn is not 9 or more bushels, however, because (1) a fall-seeded intercrop competes little or not at all with the corn and (2) full-season hybrids can be grown if the corn can be left standing for wheat seeding. The expected loss is more nearly of the order of 3 bu. The full-season hybrids average at least 6 bu. per acre more than hybrids that are early enough for harvest before wheat seeding time. The 3-bu. loss in corn yield is usually more than made up in the better wheat yields resulting from more timely seeding.

The practical applications of these modifications in row space may not survive their obvious mechanical difficulties. Again, their successful application may be geographically limited. Kiesselbach *et al.* (1935), however, suggested the possibility that double spacing of corn rows might be a practical means of facilitating wheat production in western Nebraska. Conner (1918) pointed out that the use of the wider middles gives no better corn yields in Texas, but it does favor the introduction of intertilled legume crops, reduces the cost of weed control, and sometimes provides better seedbeds for small grains.

Studies in Illinois indicate that legume intercrops have a lower competitive effect on the corn than do grasses, and that the competition is primarily for nitrogen and water in either case. With adequate nitrogen the yields of intercropped corn in 40-inch row spaces varied from about 80 per cent to practically the same as when grown under conventional systems. The Illinois workers are investigating the growing of corn in tilled slits about 20 inches wide, the slits being in a previously established sod or in a mulch obtained by mowing and chopping fall-seeded rye (Kurtz *et al.*, 1952).

VII. Choice of Hybrids

With the advent of hybrid corn, seed selection and production passed from the hands of the farmer grower to commercial seed corn producers. The several factors affecting the quality of hybrid seed are discussed in detail in Chapter IX.

Most of the factors affecting quality, such as adequacy of detasseling, careful drying and processing, and genetic merit, are not discernible in the processed seed. Therefore the farmer must select the hybrids he wishes to grow on the basis of data obtained from impartial yield trials and on his knowledge of and confidence in the merchandising agency.

VIII. Cultivation

The stirring of a rain-packed soil sometimes will be worth the effort because of improvement in aeration and receptivity to water. Wind erosion on sandy soils sometimes can be retarded temporarily by breaking up a surface crust. The control of weeds, however, is the primary objective of corn cultivation (Wirner, 1946). Cultivation beyond the requirement for controlling weeds usually does more harm than good. Effective weed control begins in those practices already described which make for good soil structure, and which leave it good through the planting preparations.

The best time to kill annual weeds is just before, or very soon after, they have emerged. On soil of good structure this job is efficiently accomplished with the wide, light-draft, fast-moving spike-tooth harrow, spring-tooth weeder, or rotary hoe. The use of one of these implements twice over, or as many times as needed, before the corn has emerged and again at about the three- or four-leaf stage is very often the most effective work done in corn cultivation. These same implements are, however, practically useless in tightly packed soil. If the packing is only in the form of a thin surface crust, the rotary hoe may break it up.

The shovel cultivator is the most effective tool when the harrow, weeder, or rotary hoe is not suitable. The wide, low-pitched, sweep-type, cultivator shovels drawn just deep enough for weed control, are excellent for early cultivation and usually for all cultivation (Jones and Beasley, 1943). But if the soil has lost structure it may be difficult to hold the low-pitched sweeps in the ground. Cultivating deeper than is required to kill weeds is bad on two counts: (1) corn roots may be cut to a harmful degree, and (2) dormant weed seeds are brought within the surface inch or so, where they will germinate.

Shedd *et al.* (1942) found that for small corn, before the six-leaf stage, the best cultivator equipment consisted of six sweeps per row and rotary-hoe shields. If the first cultivation was delayed until about the six-leaf stage, it was best to leave off the shields and use half sweeps next to the corn row. Disc hillers, replacing the two inner sweeps, were effective for later cultivations, especially if large or viney weeds were present. Shedd and co-workers also designed a spring-tooth weeder for attachment directly to the beams of the standard rear attachment for the cultivator. The weeder teeth were run close to, but not directly over, the corn plants. This attachment was recommended for all cultivations of drill-planted corn.

A ridge along the corn row is not desirable except as it may be necessary for covering weeds.

The most efficient cultivator speed can be described only as the speed at which good work is done. The temptation with tractor power is to go too fast. The speed can be increased as the corn plants are larger and the flatter sweeps can be pulled faster than high-pitched sweeps.

The use of chemical herbicides in the cornfield is relatively new, and much remains to be learned about it. Current recommendations are limited to spray applications with formulations of 2,4-D (Willard, 1953). For the present time herbicides should be looked upon as useful supplements to mechanical weed control in corn rather than as replacements for it (Helm, 1952).

The pre-emergence spray is to kill both annual grasses and broad-leaved weeds as they germinate or soon after. It should be applied after the corn has germinated but before the first leaves have unrolled. Both the ester and amine formulations of 2,4-D are used for pre-emergence application, but the esters leach less rapidly and are, therefore, less hazardous to the corn. Recommended rates range from 1 to 2 pounds acid equivalent per acre. The lower rates are used on the more porous soils. Pre-emergence treatment is hazardous on sandy soils. It will be ineffective without enough rain to leach the 2,4-D into the zone of germinating weed seeds, and it may give poor control in cloddy soil. The surface soil should not be disturbed for two to three weeks after the application.

Early post-emergence sprays are applied overall when the corn is 3 to 12 inches high. The recommendations on an acre basis are $\frac{1}{4}$ -pound acid equivalent for the esters or $\frac{1}{2}$ pound for the amine salts. This treatment is in the experimental stage. Damage to the corn is always possible if cultivation or windstorms follow treatment, and the hazard increases as the corn gets larger or encounters high temperatures.

Post-emergence treatments may be applied with drop nozzles after the corn is 1 to 2 feet high, or tall enough so that the spray can be directed toward the base of the stalk and toward the upper parts of the weeds. This treatment is often highly effective against most broad-leaved weeds, and it can be recommended where earlier control methods have failed or could not be used (Fig. 7). The recommended rates are the same as for early post-emergence treatment.

A "lay-by" spray directed at the ground and stalk bases only, and after the final cultivation, may be worth while on bottom lands. It will keep most annual weeds from becoming established for about three weeks. The esters of 2,4-D at 1 pound or the amine salts at $1\frac{1}{2}$ pounds acid equivalent per acre are recommended.

At least 5 to 10 gallons of water per acre should be used with any of the treatments referred to above. Extreme care is required in cali-

brating the spraying equipment and in maintaining correct and constant driving speeds. Spraying with 2,4-D should not be attempted if there is enough wind to carry spray to susceptible crops in other fields. Spraying should be avoided after a period of hot, moist, favorable growing weather. Cultivation is not desirable for at least a week to 10 days after spraying.

Flame weeding cannot be recommended for corn because of its high cost and the danger of injury to the crop (Lovely *et al.*, 1952).



FIG. 7. It was too wet to harrow when this corn was small. The cultivator failed to cover weeds in the drilled rows. One drop-nozzle spray application of 2,4-D was applied when the corn was 2 feet high. The blank row at the left was not sprayed.

IX. Irrigation

The use of irrigation water gives rise to a multitude of problems which cannot be discussed here. A knowledge of how corn responds to irrigation should be useful to any corn grower in the management of his soil-moisture problems, and also in the interpretation of weather in terms of probable corn crops.

Kiesselbach (1950) applied two supplemental irrigations of 3 inches each in a year of severe drought at Lincoln, Nebraska. The 6 inches of water gave a yield of 72 bu. per acre compared with no yield without irrigation. Singleton *et al.* (1950) have pointed out that corn is one of the best grain crops for irrigation because of the high yields that can be

obtained by it. They found that corn will withstand moderate drought without serious reductions in yield provided moisture is abundant through the tasseling and silking stages. But "moderate drought" apparently does not mean several days of wilting.

The effects of withholding water at various stages have been studied by Robins and Domingo (1953). A moisture deficit that caused wilting for one or two days during tasseling reduced yields up to 22 per cent, and six to eight days of wilting at this stage reduced yields about 50 per cent. Later irrigations did not make up these losses. They found, too, that removing the available water beginning four weeks after tasseling reduced yields significantly. With adequate fertilization, a stand of about 17,500 plants per acre, one preplanting irrigation, one irrigation at the tasseling stage, and two or three later irrigations, they produced yields of from 133 to 138 bushels per acre, using about 22 acre inches of water.

After long experience in irrigating corn Leonard *et al.* (1940) conclude that (1) if only one irrigation is possible, it will give the maximum grain yield if applied at the tasseling stage; (2) two irrigations are usually sufficient to produce a corn crop in Colorado, although three may be necessary on the more sandy soils; (3) corn is very sensitive to overirrigation; (4) when the corn leaves roll during the day and fail to unroll by the following morning growth has practically ceased and will not be resumed until after rain or irrigation.

Supplemental irrigation may be needed east of the normally arid or even semiarid regions. Bartholomew (1948) states that under Arkansas conditions limitations of the summer moisture supply influence corn yields more than fertility does. He obtained larger yield increases from irrigation alone than from fertilization either with or without irrigation. Luetkemeier and Konke (1949) concluded that supplemental irrigation (1) offers good possibilities for corn on the lighter textured Indiana soils even when rainfall is above average, (2) might be sound insurance against adverse dry periods on medium-textured soil, and (3) seems of questionable value on the heavier, poorly aerated soils where factors other than water appear to be the primary factors limiting corn production.

Irrigation experiments make one point clear. The most effective use of irrigation water can be realized only if the nutrient requirements of the crop are well supplied. In Mississippi Grissom *et al.* (1953) reported 36 bu. increase from 10 inches of water in a dry year where 180 pounds of nitrogen were applied per acre. The increase was only 18 bu. with 60 pounds of nitrogen.

Seed corn producers are beginning to use supplemental irrigation

even in the eastern states where the normal rainfall is 40 inches more or less. Judging from personal conversation with several of these men, the writer would conclude that the practice will be increasingly adopted.

X. Harvest

Mechanical harvest from standing stalks accounts for at least two-thirds of the ear-corn harvest in the United States. The first snapping-roller type of corn picker was invented in 1874. It was not until the dependence upon traction drive was eliminated by the development of the power take-off for tractors that the corn picker became a generally practical machine. The use of the "wagon hitch" further enhanced the practicability of machine harvest. Two-row pickers were introduced in 1928 (Hobson and Wileman, 1932).

The general farm labor shortage since the beginning of World War II coupled with the advent of hybrid corn with its superior standing ability has been of tremendous influence in the recent greatly expanded use of mechanical pickers. The saving of labor obviously depends upon factors such as size of the field, topography, type of machine, and yield and condition of the corn. Shedd *et al.* (1937) report that harvesting a 70-bushel yield of corn required 9 man-hours of labor per acre by hand harvest, compared with $2\frac{1}{2}$ man-hours by machine harvest. Richey (1943) gives the cost per hour of picker use per \$100.00 of new cost as follows: 70 cents, if the picker is used 20 hours per year; 36 cents for 40 hours annual use; 25 cents for 60 hours annual use; and 16 cents for 100 hours annual use. These costs include depreciation, repair, interest, housing, taxes, and insurance. They do not include labor or tractor-power costs. These and other similar studies (Keepper and Dum, 1948) emphasize the need for extending the use of the corn picker, and other expensive corn machinery, over as many acres and seasons as can be made practicable. About half the total cost of farm machinery is depreciation and interest (Engene and Rorholm, 1953). Methods of holding down the costs of machinery overhead are as important as any other methods in corn production. Hand work is not the answer. Making hired hands of five farmers so that the sixth can be a big operator is not necessarily the answer. Joint ownership, exchange of machines, and rental of machines work satisfactorily in some cases. But custom work is most generally followed and probably is the most generally satisfactory plan for the smaller farms. Very commonly a farmer will do custom work with perhaps a corn picker, and buy custom services of other large machines such as combines, hay balers, forage harvesters.

The custom rates for picking an acre of corn have varied during the past few years from the farm value of $2\frac{1}{2}$ to nearly 4 bushels of corn.

An additional cost lies in the fact that mechanical pickers leave more corn in the field than hand huskers do. Hobson and Wileman (1932) found that hand huskers left an average of 2.75 per cent, compared with 7.70 per cent for one-row pickers and 9.90 per cent for two-row pickers.

Smith *et al.* (1949) found (1) little difference between drilled and checked corn in terms of picker efficiency and (2) a reduction of 20 per cent in losses of shelled grain by reducing the speed of travel to low gear. They also found (3) that shelling losses were inversely related to kernel-moisture content, the loss rising very sharply when kernel moisture dropped below 15 per cent, and (4) that both shelling and ear droppage increased as harvest was delayed beyond maturity.

Bateman *et al.* (1952) report losses in corn yielding 80 bu. per acre, (1) of 1.33 bu. per acre for each increase of one-eighth inch in the space between the snapping rolls beyond that necessary to prevent clogging, (2) of 2.7 bu. per acre when changing from first tractor gear to the second gear. The same authors state that corn lost by pickers averages 10 per cent of the yield, mostly within the range of 5 per cent to 20 per cent. Modern pickers can do better than that if given a fair opportunity by good adjustment, careful driving, moderate speed, timely harvest, and corn on nonrotted stalks (Fig. 8).

It is clear that the selection of a custom operator usually will be determined more by the quality of his work than by his acreage fee. Furthermore, he will be unable to do an efficient job if the stalks are disintegrating.

Combination picker shellers are too new for objective evaluation at this time. They can be expected to find their first economical use toward the western corn-producing areas where natural drying is most effective, and where corn production is on a relatively large scale. The machines now available will harvest grain carrying about 27 per cent or less of moisture. The grain is then artificially dried.

Corn harvested for silage amounts to about 6 per cent of the total crop. Wisconsin is the leading state in the production of corn silage, putting nearly half its corn crop in about 130,000 silos. The Wisconsin Experiment Station (Allen *et al.*, 1951) recommends that the best time to make silage is when one-fourth of the kernels have begun to dent. Minimum nutrient loss will be had if harvest is at this time. Earlier harvest is recommended, however, (1) if the plants begin to dry because of drought, or (2) if a freeze has occurred, in which case harvest should follow as soon as practicable. Kiesselbach (1950) describes the denting stage as the period when the grain contains 56 per cent of moisture, which is about a week before the glazing stage, and about two

weeks before the ripe stage (34 per cent kernel moisture). The highest yield of feed constituents ordinarily will be had by harvesting in the glazing stage. The preferred method is to grow a hybrid that is 5 to 10 days later than would be used for grain. A hybrid of this maturity will reach the early dent stage before serious frost hazard in most seasons, and it will yield as much feed when harvested at the early dent stage



FIG. 8. Good cultural practices and good heredity are back of this ripened crop. The stalks are still sound and will stand until delayed harvest if it is required.

as would a midseason hybrid that was allowed to stand until nearly mature (Wiggans, 1937).

The most modern method of harvesting corn silage is with a field silage chopper equipped with a blower that loads a wagon which is pulled behind. The chopped corn is then promptly transferred to a silo filler with the aid of a mechanical unloader. The field silage choppers, wagons with mechanical unloading devices, and the silo fillers often are owned by custom operators.

Harvesting corn with livestock accounts roughly for another 6 per cent of the corn in the United States. Hogs harvest the crop with fair efficiency if the ground is reasonably dry and if the hogs can be confined to small areas which they will clean up thoroughly before being moved to a fresh area. The inconvenience in supplying supplements and water and of moving fences and shelters seems to be the principal deterrent to this method of harvest. Lambs harvest corn with somewhat less efficiency than hogs; and cattle, with less efficiency than lambs. Hogs following the lambs or along with the cattle improve the efficiency. The tramping of cattle may break down the structure of wet soil. Hogs and lambs may do the same, but to a lesser extent.

XI. Farm Drying and Storage

The problems of farm storage center on drying, protection against rodents and storage insects, and adequate mechanical construction of storages (Shedd, 1949).

Dependence on sun and air for drying is cheapest and most common among American farmers. The corn is stored on the ear in cribs having walls of spaced slats, wire mesh, or louvered steel (Fig. 9).

Horizontal strength in corn storages is important and often inadequate. Horizontal pressures appear to be greater than would be expected if only the weight of the corn were involved. They may have their origin partly in the recurrent settling and swelling accompanying changes in atmospheric humidity.

The safe kernel moisture content for ear corn at cribbing time is about 20 or 21 per cent. It will be higher by several per cent (1) if thorough cross ventilation is provided with open-slatted or steel ventilators placed within 3 or 4 feet of each other, and if the corn is free of debris, or (2) if the storage is to be limited to cold weather.

Recommended crib widths for natural drying of ear corn are 5 to 6 feet in a belt extending from the northern half of Pennsylvania northwesterly across central Minnesota. Crib widths may be wider toward the south and west from this belt, the width reaching 10 feet in central Kansas and western Nebraska. The diameter of round cribs may be about a half greater than the width of rectangular cribs.

Effective drainage, liming, and good fertilization all contribute important insurance against delayed ripening and wet corn at harvest time. Good soil structure improves the chances for thorough early control of weeds. Weed seeds and weed trash often are largely responsible for poorly ventilating cores where the corn drops into the cribs from elevator spouts. Ventilating air bypasses the core and spoilage ensues. Good drying is aided by the selection of a hybrid that normally reaches ma-

turity in time for safe farm storage and that will stand without early stalk disintegration if delayed harvest is necessary.

Clean husking and clean corn in the crib are necessary for good drying and, of course, there must be provision for ventilating air. Natural ventilation will be better if the crib is away from trees or other buildings, and the fire hazard will be reduced thereby.



FIG. 9. Efficient one-man operation. The crib is well away from trees and other buildings providing good ventilation. It is well constructed. The ends of steel cross ties can be seen on the right side wall. The crib floor is well off of the ground and free of rat harbors beneath. The elevator is provided with a screen to sift out shelled grain and fine trash.

Drying corn on the farm with forced ventilation is gaining favor (Holman, 1951). Portable heaters and blowers are available which can be attached to a wide variety of cribs even though the cribs were designed for natural ventilation. If a new storage is to be built, it would be well to consider using forced ventilation so that a maximum of efficiency can be realized.

Forced unheated air usually will not be profitable at air temperatures below 50°F., and it cannot be used in rainy or foggy weather, since it would only make the corn wetter. Unheated air is likely to be practical in areas where bright warm fall days are the rule, but even there it fails to free the farmer from dependence upon the weather for drying.

If the farmer is equipped to dry with heated air, he is (1) almost independent of weather, (2) well insured against storage losses in "soft-corn" years, (3) in position to harvest earlier, or to grow later and higher yielding hybrids, (4) prepared to store in tight bins for fumigation to control insects, and (5) equipped to preserve the high quality of newly harvested grain. Batch drying permits immediate cooling and removal to tight bins, permanent storage, or market.

Heated air can be used for drying corn either on the ear or after shelling. Shelled grain can be dried more cheaply than ear corn because it is not necessary to dry the cobs. Cobs are wetter at harvest than the grain. Objections to drying with heated air are: (1) the extra supervision and labor required, (2) power and fuel costs, (3) increased fire hazard, and (4) possible losses in cash returns if the corn is marketed drier than is required for the grade. Furthermore, both the wet millers and the dry millers of corn prefer naturally dried grain (MacMasters, 1953). If corn has been dried too fast, the outer part of the kernel develops minute cracks, and on dry milling the endosperm (starch portion) may crumble. That is undesirable. The wet-milling process is exceedingly difficult with corn grain that has been overheated. The protein and starch will not separate into relatively clean fractions, the dead germ is difficult to remove as a whole, and the oil is low in grade and difficult to recover. There is evidence, too, that high drying temperatures may decrease the feeding value of the protein (Hathaway *et al.*, 1952). It would seem wise, therefore, to hold the drying temperatures down as much as is consistent with efficient operation. Speed in farm drying rarely will be so urgent that the temperature of the heated air will need to be higher than 130°F.

Protection against storage insects is best accomplished by fumigation in tight bins (Cotton, 1952). If infestation occurs in the field it is recommended that harvest be as early as practicable. If the corn is not dry enough at harvest for tight-bin storage, it may be possible to fumigate in batches before storing in ventilated storage cribs, after they have been made temporarily airtight by fastening tarpaulins, felt, or heavy paper, on the side walls. If the floor is tight, fumigants that are heavier than air can then be used.

Where storage insects are a perennial threat, as in some of the south-

ern states, the following procedure would seem worth while: (1) harvest early, (2) dry with forced, heated air, (3) shell, (4) clean with fan, (5) store in a tight bin, and (6) fumigate. Or, depending upon the type of equipment, shelling may precede drying.

Rats could scarcely be tolerated if they only ate. But they foul more than they eat. No building can be called a corn storage without adequate protection against them. Rat protection can be achieved with this combination: (1) concrete foundations, 2 feet deep, (2) concrete floors, (3) a 2-foot strip of wire mesh attached to the lower side walls (if the walls are slatted) topped with a 6-inch strip of galvanized metal, (4) freedom from board piles and other harbors alongside the storage. Many farmers have had complete rat protection by setting their corn storages on piers 2 feet high, then keeping the space beneath the storage free of boards or other convenient harbors. Sometimes each pier is topped with an overhanging sheet of galvanized metal. The use of motor-driven elevators makes this plan practical for the smaller storages.

REFERENCES

- ALLEN, N. N., BOHSTEDT, C., NEAL, N. P., PETERSON, W. H., PHILLIPS, P. H., STROMMEN, A. M. and WITZEL, S. A. 1951. Kernels are the key to good corn silage. *Univ. Wisconsin Agr. Exp. Ser. Circ.* **337** (Revised).
- BARTHOLOMEW, R. P. 1948. Increasing corn yields in Arkansas. *Arkansas Agr. Expt. Sta. Bull.* **473**.
- BATEMAN, H. P., PICKARD, G. E., and BOWERS, W. 1952. Corn picker operation to save corn and hands. *Univ. Illinois Agr. Ext. Circ.* **697**.
- BEAR, F. E. 1953. "Soils and Fertilizers," 4th ed. John Wiley & Sons, New York.
- BORST, H. L., and VOLK, G. W. 1952. Mulching corn with manure for erosion control. *Ohio Agr. Expt. Sta. Agronomy Series No.* **125**.
- BORST, H. L., and WOODBURN, R. 1942. The effect of mulching and methods of cultivation on runoff and erosion from Muskingum Silt Loam. *Agr. Eng.* **23**: 19-22.
- BRADFIELD, R. 1952. Water . . . Life blood of your soil! *What's New in Crops and Soils* **5**: 15.
- CONNER, A. B. 1918. Spacing of rows in corn and its effects upon grain yield. *Texas Agr. Expt. Sta. Bull.* **230**.
- COOK, R. L., and PEIKERT, F. W. 1950. A comparison of tillage implements. *Agr. Eng.* **31**: 211-214.
- COTTON, R. T. 1952. Fumigating stored foodstuffs. *Yearbook Agr. U. S. Dept. Agr.*, pp. 345-349.
- DULEY, F. L., and RUSSELL, J. C. 1939. The use of crop residues for soil and moisture conservation. *J. Am. Soc. Agron.* **31**: 703-709.
- DUMENIL, L. 1952. Nitrogen fertilizers for corn. *Iowa Agr. Expt. Sta. Bull.* **P114**.
- ENGINE, S. A., and RORHOLM, N. 1953. Machinery—servant or master. *Minnesota Farm and Home Sci., Minnesota Agr. Expt. Sta.* **2**: 4-5.
- GRAY, R. B. 1938. Tillage machinery. "Soils and Men." *Yearbook Agr. U. S. Dept. Agr.*, pp. 329-346.
- GRISSOM, P. H., RANEY, W. A., DICKERSON, R. O., KELLY, J. F., BENNETT, H. W.,

- HARRIS, V., JORDAN, H. V., HOGG, P. G., and EDWARDS, F. E. 1953. Crop response to irrigation. Mississippi Farm Research. *Mississippi Agr. Expt. Sta.* **16** (3): 5.
- HASWELL, JOHN R. 1938. Drainage in the humid regions. "Soils and Men." *Yearbook Agr. U. S. Dept. Agr.*, pp. 723-736.
- HATHAWAY, I. L., YUNG, F. D., and KIESSELBACH, T. A. 1952. The effect of drying temperature upon the nutritive value and commercial grade of corn. *Animal Sci.* **2**: 430-440.
- HELM, C. A. 1952. Weed control in corn through use of chemicals. *Univ. of Missouri, Agr. Ext. Circ.* **619**.
- HOBSON, L. G., and WILEMAN, R. H. 1932. Mechanical corn pickers in Indiana. *Indiana Agr. Expt. Sta. Bull.* **362**.
- HOLMAN, L. E. 1951. Artificial drying of grain crops. *What's New in Crops and Soils* **4**: 9-13.
- JENKINS, M. T. 1934. A comparison of the surface, furrow, and listed methods of planting corn. *J. Am. Soc. Agron.* **34**: 734-737.
- JENNY, H. 1930. A study of the influence of climate upon the nitrogen and organic matter content of the soil. *Missouri Agr. Expt. Sta. Research Bull.* **152**.
- JOHNS, D. M., and BROWN, H. B. 1941. Effect of date of planting on corn yields, insect infestation, and fungous diseases. *Louisiana Agr. Expt. Sta. Bull.* **327**.
- JONES, M. M., and BEASLEY, R. P. 1943. Corn tillage studies on rolling Putnam Silt Loam. *Missouri Agr. Expt. Sta. Bull.* **475**.
- JORDAN, H. V. 1951. Fertilizer and production practices for corn in the hill sections of Mississippi. *Mississippi Agr. Expt. Sta. Bull.* **486**.
- KEEPPER, W. E., and DUM, S. A. 1948. Costs and labor used in harvesting corn grain and stover. *Pennsylvania Agr. Expt. Sta. Bull.* **496**.
- KIESSELBACH, T. A. 1950. Progressive development and seasonal variations of the corn crop. *Nebraska Agr. Expt. Sta. Research Bull.* **166**.
- KIESSELBACH, T. A., ANDERSON, A., and LYNESS, W. E. 1935. Cultural practices in corn production. *Nebraska Agr. Expt. Sta. Bull.* **293**.
- KIESSELBACH, T. A., and LYNESS, W. E. 1952. Crop rotation experiments. *Nebraska Agr. Expt. Sta. Bull.* **416**.
- KNOBLAUCH, H. C. 1942. Contour tillage of corn under New Jersey conditions in relation to soil and water conservation, crop yields, and various soil properties. *J. Am. Soc. Agron.* **34**: 263-269.
- KRANTZ, B. A. 1949. Fertilize corn for higher yields. *North Carolina Agr. Expt. Sta. Bull.* **366**.
- KURTZ, T., MELSTED, S. W., BRAY, R. H., and BRELAND, H. L. 1952. Further trials with intercropping of corn in established sods. *Soil Sci. Soc. Amer. Proc.* **16**: 282-285.
- LEONARD, W. H., BRANDON, J. F., and CURTIS, J. J. 1940. Corn production in Colorado. *Colorado Agr. Expt. Sta. Bull.* **463**.
- LOVELY, W. G., SYLWESTER, E. P., STAINFORTH, D. W., COLLINS, E. V., and BALKE, A. L. 1952. How to control weeds in corn. *Iowa Farm Sci., Iowa Agr. Expt. Sta.* **11**: 185-188.
- LOWREY, G. W., and EHLERS, P. L. 1952. Fertilizer experiments with corn in central and eastern Nebraska. *Nebraska Agr. Expt. Sta. Outstate Testing Circ.* **27**.
- LUETKEMEIER, O. W., and KONKE, H. 1949. The influence of supplemental irrigation on corn yields in Indiana. *Soil Sci. Soc. Amer. Proc.* **14**: 379-383.
- MACMASTERS, M. M. 1953. Grain structure and grain storage. *U. S. Dept. Agr., Northern Reg. Research Lab., Peoria, Illinois, AIC* 348.

- MANGLESORF, P. C. 1929. Corn varieties in Texas; their regional and seasonal adaptation. *Texas Agr. Expt. Sta. Bull.* **397**.
- MARRIOT, L. F., and JACKSON, M. L. 1952. Use of commercial nitrogen on field crops. *Dept. of Soils, Univ. of Wisconsin. A. E. S. Project 693e—Rept. for 1952* (mimeographed).
- MCVIKAR, M. H. 1952. "Using Commercial Fertilizer," 1st ed., pp. 43–57. Interstate, Danville, Illinois.
- MILES, S. R. 1951. Rate and pattern of planting corn. *Proc. Sixth Ann. Hybrid Corn Industry-Research Conf.* **6**: 68–81.
- NICHOLS, M. L., and CHAMBERS, T. B. 1938. Mechanical measures of erosion control. "Soils and Men." *Yearbook Agr. U. S. Dept. Agr.*, pp. 646–665.
- NORTON, R. A., COLLINS, E. V., and BROWNING, G. M. 1944. Present status of the plow as a tillage implement. *Agr. Eng.* **25**: 7–10.
- Ohio Experiment Station. 1951. Ohio experiments in agronomy. Book series B-1, Wooster, Ohio.
- PAGE, J. B., and WILLARD, C. J. 1946. Cropping systems and soil properties. *Soil Sci. Soc. Amer. Proc.* **11**: 81, 88.
- PENDLETON, J. W., DUNGAN, G. H., KOEHLER, B., BIGGER, J. H., LANG, A. L., and JOHNSON, P. E. 1952. Illinois corn tests. *Illinois Agr. Expt. Sta. Bull.* **564**.
- PORTERFIELD, J., and HULL, D. 1952. How much does custom work cost? *Iowa Farm Sci., Iowa Agr. Expt. Sta.* **6**: 101–103.
- PRINCE, A. L., TOTH, S. J., BLAIR, A. W., and BEAR, F. E. 1941. Forty-year studies of nitrogen fertilizers. *Soil Sci.* **52**: 247–262.
- RICHEY, C. B. 1943. Cost per hour of using farm machinery. *Ohio State Univ., Agr. Ext., Ser. Bull.* **221**.
- ROBERTSON, W. K., and OHLROGGE, A. J. 1952. An evaluation of methods of side-dressing corn with nitrogen. *Agron. J.* **44**: 170–172.
- ROBINS, J. S., and DOMINGO, C. E. 1953. Some effects of severe soil moisture deficits at specific growth stages in corn. *Agron. J.* **12**: 618–621.
- ROGERS, J. S., and COLLIER, J. W. 1952. Corn production in Texas. *Texas Agr. Expt. Sta. Bull.* **746**.
- ROUNDS, W. T., ROSSMAN, E. C., ZURAKOWSKI, W., and DOWN, E. E. 1951. Rate, method, and date of planting corn. *Michigan Agr. Expt. Sta., Quart. Bull.* **33**: 372–387.
- SALTER, R. M., LEWIS, R. D., and SLIPHER, J. A. 1936. Our heritage—The soil. *Ohio Agr. Expt. Bull.* **175**.
- SCOFIELD, C. S. 1938. Soil, water supply, and soil solution in irrigation agriculture. "Soils and Men." *Yearbook Agr. U. S. Dept. Agr.*, pp. 704–716.
- SCHALLER, F. W. 1951. Plow, list, or disc? *Iowa Agr. Expt. Sta. Iowa Farm Sci.* **5**: 175–178.
- SCHALLER, F. W., and PROJECT LEADERS. 1953. Annual Progress Report, Western Iowa Expt. Farm. FER-70. Iowa State College.
- SHEDD, C. K. 1949. Storage of ear corn on the farm. *U. S. Dept. Agr., Farmers' Bull.* **2010**.
- SHEDD, C. K., COLLINS, E. V., and DAVIDSON, J. B. 1937. Labor, power, and machinery in corn production. *Iowa Agr. Expt. Sta. Bull.* **365**.
- SHEDD, C. K., COLLINS, E. V., and DAVIDSON, J. B. 1942. Weed control in growing corn. *Iowa Agr. Expt. Sta. Bull.* **P44**.
- SINGLETON, H. P., VIETS, F. G., LEAMER, R. W., MENZLES, J. D., NELSON, C. E., CLORE, W. J., LARSON, C. A., DOMINGO, C. E., and OLSEN, S. R. 1950. Soil, water,

- and crop management investigations in the Columbia Basin Project. *Washington Agr. Expt. Sta. Bull.* **520**.
- SLIPHER, J., and SILVER, E. A. 1951. Plowman's purpose. *Farm Implement News*, July 10, 1951, Chicago 5, Ill.
- SMITH, C. W., LYNESS, W. E., and KIESSELBACH, T. A. 1949. Factors affecting the efficiency of the mechanical corn picker. *Nebraska Agr. Expt. Sta. Bull.* **394**.
- SMITH, D. D., WHITT, D. M., and MILLER, M. F. 1948. Cropping systems for soil conservation. *Missouri Agr. Expt. Sta. Bull.* **518**.
- SMITH, G. E. 1952. Soil fertility and crop production. *Missouri Agr. Expt. Sta. Bull.* **583**.
- STACY, S. V. 1941. Corn varieties, hybrids, and cultural practices. *Georgia Expt. Sta., Univ. Georgia Circ.* **126**.
- STRINGFIELD, G. H., and THATCHER, L. E. 1947. Stands and methods of planting for corn hybrids. *J. Am. Soc. Agron.* **11**: 995-1010.
- STRINGFIELD, G. H., and THATCHER, L. E. 1951. Corn row spaces and crop sequences. *Agron. J.* **43**: 276-281.
- THORP, J., and SCOFIELD, C. S. 1938. Drainage in arid regions. "Soils and Men." *Yearbook Agr. U. S. Dept. Agr.*, pp. 717-722.
- TRUOG, E., BERGER, K. C., ENGELBERT, L. E., and PETERSON, A. E. 1953. Writing the fertilizer prescription on basis of soil tests. *Am. Soc. Agron. Abstracts*. 1953. Annual Meetings. pp. 54-55.
- UHLAND, R. E. 1949. Physical properties of soils as modified by crops and management. *Soil Sci. Soc. Amer. Proc.* **14**: 361-366.
- VAN BAVEL, C. H. M., and SCHALLER, F. W. 1950. Soil aggregation, organic matter and yields in a long-time experiment as affected by crop management. *Soil Sci. Soc. Amer. Proc.* **15**: 399-404.
- VAN DOREN, C. A., STAUFFER, R. S., and KIDDER, E. H. 1950. Effect of contour farming on soil loss and runoff. *Soil Sci. Soc. Amer. Proc.* **15**: 413-417.
- WIGGANS, R. G. 1937. The influence of stage of growth of corn on the composition of silage. *J. Am. Soc. Agron.* **29**: 456-467.
- WILLARD, C. J. 1953. Chemical weed control in field crops. *The Ohio State Univ. Agr. Ext. Bull.* **337**.
- WIRNER, D. C. 1946. Why cultivate corn? *Univ. Illinois, Coll. Agr., Circ.* **597**.
- YODER, R. E. 1936. A direct method of aggregate analysis of soils and a study of the physical nature of erosion losses. *J. Am. Soc. Agron.* **28**: 337-351.
- ZINGG, A. W. 1940. Degree and length of slope as it affects soil loss in runoff. *Agr. Eng.* **21**: 59-64.

CHAPTER IX

Production of Hybrid Corn Seed

JOHN M. AIRY¹

I. Seed Corn Producers and Production Practices

A new business devoted to the growing, sale, and distribution of hybrid corn seed has developed following the general adoption of hybrid corn in American agriculture. Hybrid corn requires new F_1 seed each year. A yield reduction of 15 to 20 per cent results from use of F_2 double-cross seed (Richey *et al.*, 1934; Sprague, 1942). Annual hybrid corn seed requirements of the United States are about 9 million bushels.

In 1933 only 1 per cent of the corn acreage in the Corn Belt was planted with hybrid corn seed. In 1953 it was estimated that 96 per cent of the acreage in the Corn Belt and 86 per cent of the national corn acreage was planted with hybrid corn seed (Anonymous, 1953). The hybrid corn seed producer grows many hybrids, differing in many characteristics, especially in area of adaptation or maturity. The hybrids are highly selected—the result of breeding and testing programs conducted by Federal, state, and private corn breeders.

1. Large and Small Growers

A large number of individuals, partnerships, and corporations have developed a business in hybrid corn seed. Such a firm usually establishes a sales and a distribution program for marketing the seed it produces. Similar trends and developments in hybrid corn seed are now apparent in other corn-growing areas of the United States, particularly in the south. This discussion will be devoted primarily to experience in the Corn Belt.

In the beginning all seed corn firms were small. Each was inexperienced and uncertain what standards were necessary to produce a high-quality product and yet avoid expense of no economic value to the customer. During the development period, prior to 1940 to 1942, the certi-

¹ The author acknowledges associates in Pioneer Hi-Bred Corn Company, Mr. S. F. Goodsell, Mr. George Huey, and Mr. Delmar Henderson, who have done much of the work referred to as unpublished data. As used herein, unpublished data refers to experimental results on file at Johnston, Iowa, but not published.

fication program, sponsored by crop improvement associations under the auspices of the various land-grant colleges, was a co-ordinating and an educational influence in the development of satisfactory production methods. In the early day before brand names were established, the blue tag of certification was an aid to the customer in selecting proved hybrids and in selecting good sources of seed corn. As producers gained experience, acquired capital, and developed merchandising programs, a large number found it necessary to produce and to distribute under private brand names. Customer preference developed. Large expenditures were made in the field of private research, supplementing the state and Federal corn-breeding programs. By 1945 a small group of corporations emerged as major producers of seed corn for the Corn Belt.

2. *Role of Certification*

Most land-grant colleges of the nation have sponsored a private non-profit corporation, the *crop improvement association*, often supported in part by state appropriations. Its purpose is to identify superior varieties of many crops, such as clover, alfalfa, brome grass, oats, wheat, potatoes, etc., and to certify that certain practices were followed in the production and labeling of these varieties. Both "open pedigree" corn hybrids, developed by state and Federal research, and "closed pedigree," or private brand corn hybrids, may be certified in most states. The seedsman desiring to certify applies for the certification service and pays a fee covering most of the cost of the service. In most states the only legal regulation is that the right to use a blue tag is limited to "officially certified seed."

There are four main phases of the certification program as it applies to hybrid corn seed: (1) to identify hybrid varieties that have shown superiority in performance in official tests, except that some states do not include in such tests "private brand" hybrids from out-of-state producers and a few exclude even those from intrastate producers; (2) to identify the maturity adaptation of the variety; (3) to assure that the seed stock used for planting the seed field was certified and produced according to certain standards; (4) to assure that the production—particularly isolation of seed fields, detasseling, and germination of the double-cross seed—was according to specified standards; and (5) to issue blue certification tags to the producer for the labeling of seed which has passed certification requirements.

The International Crop Improvement Association issues certification requirements that are regarded as the minimum to be used by state members of the association.

The certification program of corn is an important factor in the production and distribution of both inbred seed and single-cross seed. The limitation of certification with respect to double-cross seed is that two producers, growing seed of the same hybrid under the certification program, may still deliver to the customer products that are quite different in performance, particularly in stand obtained under cold wet spring planting conditions (Rinke, 1953). Seed from different producers differs in germination potential (Airy, 1947). Certification is a partial assurance of quality, not a guarantee; the customer must evaluate the seed, in part, according to the ability and reputation of the producer.

3. Hybrid Corn Seed Industry

The first plot for crossing inbred lines by detasseling was at the Connecticut Agricultural Experiment Station at Mount Carmel in 1916. The first crossing field for production of hybrid seed, a cross of BURR-LEAMING, was grown at Clinton, Connecticut, in 1921, producing about 8 bu. of seed. The second hybrid to be produced and the first to be sold commercially was a 40-acre seed field crossed by detasseling near Des Moines, Iowa, in 1923; it was sold for planting in 1924 under the name "COPPER CROSS," a cross between a LEAMING inbred line produced by the Connecticut Station and an inbred from CHINESE BLOODY BUTCHER produced by H. A. Wallace. The first seed company for commercial production of hybrid corn seed was organized in Iowa in 1926 (Jenkins, 1936).

The larger seed corn producers in the Corn Belt conduct a complete hybrid corn program. Research departments conduct research in the development of inbreds, production and testing of experimental crosses, and selection of hybrids of merit for various areas according to maturity adaptation. The firms increase inbred seed stocks, grow the needed single-cross seed stocks, produce double-cross seed, sell the seed through salesmen who call directly on the farmer, and deliver the seed to the salesmen according to their actual sales by submitted orders.

The larger corporations conduct this type of program as a single unit. The medium-sized corporations or producers have independent production and sales programs, but in some cases conduct a co-ordinated research program as a group.

The small producer, perhaps 20,000 bu. or less—usually much less—operates independently. He may carry on limited research efforts but depends largely upon the state colleges and the United States Department of Agriculture for research, hybrid development, and local performance testing.

II. Seed Stock Increase

Specialized producers make a business of producing and selling inbred and single-cross seed. Seed stock increase, sometimes called parent corn production, is a department within the larger companies.

1. *Inbred Increase*

Inbred lines are maintained by continued selfing of representative plants, or by careful roguing for plant type and then sibmating between plants in the row. Generally, those following the latter program alternate between sibbing and selfing to control outcrossing.

Inbred lines may be increased by hand-pollination or by growing the inbred in an isolated plot. Common practice is to increase the inbred by an isolated plot or small field and by hand-pollinating within the plot. The hand-pollinated seed is held for planting future inbred increase plots, and the inbred seed crop is used for producing single crosses.

2. *Single-Cross Seed Production*

Single-cross seed produced for sale on the market is usually certified, since certified single-cross seed is required for producing certified double-cross seed. Standards for single-cross seed production are more strict as to isolation, purity of plant type, and purity of ear type than standards for double-cross seed. Practices followed by companies for private use with noncertified seed are similar to certification requirements. Purchasers of single-cross seed evaluate seed sources on the integrity and the ability of the producer whether or not the seed is certified.

Single-cross seed is borne on an inbred plant. Thus the yield per acre is low, the kernels are often odd-shaped, and special attention must be given to time of harvest, freeze damage to germination, drying temperature, handling damage, storage temperature, and seed treatment.

The cost of inbred seed varies greatly, with no standard pricing practice. Single-cross seed is priced in units of 1000 viable kernels, about 50 to 60 cents per unit in 1953.

III. Planting and Growing Seed Corn

Agronomic practices followed in growing a seed field are essentially the same as for growing a good crop of corn for feed. In addition, there are some special activities because it is seed corn. Most producers determine the seed field acreage to be planted as that needed to produce a given volume of seed based on normal yields. Thus they are anxious to reduce risk of low yields to a minimum. Crop risk is reduced by (1)

selection of high-yielding areas within the state, (2) selection of good fields within a growing area, (3) selection of good farmers, (4) avoidance of droughty or light soil, poorly drained fields, or fields subject to flooding, (5) planting of stands which are adequate but not heavy enough to increase the risk of drought damage, (6) use of a balanced fertilizer program of both starter and broadcast fertilizers, (7) control of insects, especially soil-borne insects, cutworms, and corn borers, through use of chemicals, and (8) emergency use of herbicides, such as 2,4-D, for weed control.

1. Isolation of Seed Fields

Seed fields are planned with isolation of 40 rods as the base distance from other corn. The distance is modified according to field size and by planting border rows on sides of the field exposed to other corn. Isolation standards are, apparently, based on practical experience rather than on experimental evidence (Gacitua, 1946).

Studies confirm that greatest contamination occurs in the 10 to 15 rods nearest contaminating corn, that dilution of contamination by pollen from border rows occurs, that tree barriers may reduce contamination for 10 to 15 rods, that an abundant supply of male corn pollen at the right time is an important factor in contamination in seed fields, that direction from contaminating corn influences amount of contamination, and that "depth of field" in the direction of contaminating corn is of importance in reducing contamination (Gacitua, 1946; Airy, 1950; Jones and Brooks, 1950; Jones and Brooks, 1952).

a. Isolation from White Corn, Sweet Corn, and Popcorn. Seed fields of yellow corn are usually isolated at least 80 rods from white corn, sweet corn, or popcorn fields. In most instances white corn contamination can be observed by kernels with a white crown. Areas with excessive contamination are usually abandoned. Sweet corn patches in gardens within the 40-rod isolation distance are usually removed or detasseled.

b. Isolation of White Corn Hybrid Seed Fields. The isolation of seed fields of white corn hybrids is a special problem. Forty rods is regarded as an absolute minimum distance from yellow corn. Isolation of 80 rods or more is preferred. White corn seed fields are often grown in areas where white corn is commonly grown, so that contamination will be from white corn and will not be so undesirable to the customer. Some producers of white corn hybrid seed use an electric eye sorting device for removing the kernels pollinated by yellow corn pollen. These machines operate on the basis of passing each kernel through a beam from the electric eye. The presence of dark-colored kernels activates a me-

chanical device which separates these kernels from the flow or supply of white kernels.

2. Row Ratio in Seed Fields

The row ratio in single-cross seed fields is usually two rows of female corn to one row of male (Fig. 1), occasionally four rows of female to two rows of male, and with a few producers two rows of male to two rows of female. Planting half the field to male corn supplies larger amounts of male corn pollen, assuring greater purity in the cross.



FIG. 1. A field for crossing two inbreds to produce single-cross seed, usually planted two rows of ear parent to one row of female parent and usually isolated 40 rods or more from other corn.

Double-cross seed fields are generally planted six rows of female to two rows of male corn (Fig. 2). Occasionally, the ratio is eight rows of female to two rows of male. When the male corn is lacking vigor, is planted at a different date, or tends to shed limited amounts of pollen, the row ratio is reduced to four rows of female corn to two rows of male corn. Female corn is the line used for ear parent—the detasseled rows. Male corn is the line planted as a pollen source—the ears are used only for feed. The producer chooses the line to be used as rows of female corn and the line to be used as rows of male corn.

Unpublished data suggest that a row ratio of eight to two may result in a smaller percentage of flat kernels on ears from center rows in the female blocks when pollen supply and timing from the male rows is not ideal.

3. Soil Fertility in Seed Fields

High yields in seed fields contribute to lower seed costs per bushel of seed, since fixed costs, such as detasseling, are about the same whether

the yield is high or low. In addition, high seed field yields contribute to plump, sound seed and early maturity.

Seed fields are located on farms with a high level of fertility, operated by good farmers with adequate equipment. Well-drained farms where the farmer has followed good conservation practices, has used legumes in rotation, has used lime to correct acidity, and uses fertilizers effectively, are favored. The soil test technique is now being used to estimate the nitrogen, phosphate, and potash needs for the soil. Starter fertilizer is used on most seed fields. The seed producer works closely



FIG. 2. A field for crossing two single crosses to produce double-cross seed, usually planted six rows of ear parent to be detasseled (female) to two rows of pollen parent (male). Photo shown is four female rows to one male row.

with state experiment stations and fertilizer companies, conducts test plots on fertilizer use, and encourages each grower to experiment with strip tests to learn the best soil fertility and fertilizer practices applicable to his farm. High seed field yields, by efficient and practical methods, benefit both the contract grower and the seedsman.

4. Planting the Seed Field

Planting in early May in Iowa gives maximum yields (Sprague *et al.*, 1950; Dungan, 1944) and results in reduced moisture at harvest (Dyas *et al.*, 1952), both in spite of increased risk of stand reduction from seed rot and soil-borne insects and risk of increased corn borer infestation. Unpublished data (Iowa State College, 1953) give seven-year average yields for ten hybrids for four planting dates—about May

7, May 16, May 26, and June 4—as 88.2, 91.1, 88.8, and 84.3 bu., respectively. During the years 1950, 1951, and 1952, one half of each plot was sprayed with DDT, as for first-brood corn borer, with yield increases of 9.9, 5.7, 1.7, and 3.1 bu., respectively, even with little or no corn borer infestation. A six-year average—1946 through 1951—for the same test gave moisture percentages at harvest of 18.5, 19.7, 21.4, and 23.0, respectively.

Planting rate is planned to give optimum yields, but excessive stands are avoided to reduce drought risk and to avoid small nubbin-type ears. Many investigators have studied the effect of planting rate on yield, with recent investigations studying planting rate in relation to level of soil fertility. A limited survey shows that in Iowa, Illinois, and Indiana the preferred stand for seed fields is about 12,000 to 14,000 plants per acre. Stand is adjusted upward if the fertility level of the farm, combined with the fertilizer practices being used, seems to justify the added stand. The maximum stand desired in seed fields is about 16,000 plants per acre.

5. *Heat Units as an Index on Rate of Growth*

The sweet corn canning industry has developed a *heat unit method* to time the delay in planting fields of peas and sweet corn to give a regular schedule of number of acres reaching maturity on succeeding days during harvest. Literature shows the relation of development of sweet corn and peas to the summation of temperature units during growth (Magoon and Culpepper, 1932; Katz, 1952).

The *heat unit* is an index or summation of degree day units wherein the daily average temperature exceeds 50°F.—generally regarded as minimum temperature for growth of corn. For instance, with a high of 100°F. and a low of 60°F., 30 heat units have occurred; or with 60°F. high and 40°F. low, 0 heat units are assumed. This temperature range for growth of corn is recognized as varying somewhat from the limits given (48°F. to 50°F.), but proves sufficiently accurate for such calculations. The method has limitations but can aid the seedsman in timing delay of planting when lines differ in time of flowering and in estimating time of detasseling of seed corn or time of harvest of sweet corn.

Unpublished data show stability of the index in that the mean heat units for 50 inbreds for five years for each of three planting dates were: early (May 12–17), 1703; medium (May 22–27), 1708; and late (June 1–6), 1706. The mean heat units by years for the same 50 inbreds with three planting dates were: 1946, 1748; 1947, 1862; 1948, 1705; 1949, 1701; and 1950, 1512. Statistical analysis shows that variation from planting date within a season and variation from hybrids planted on

different dates within a season were both not significant. Significant sources of variation were from lines, years, interaction of dates by years, and interaction of lines by years. Seed field records in 1950 gave a standard deviation of about 50 heat units for time of detasseling of single fields as compared with the variety mean, based on 128 fields and 7 hybrids.

6. Insect Control in Seed Fields

Control of cutworms, wireworms, webworms, corn borer, seed-corn beetle, seed-corn maggot, and other corn insects by use of chemicals

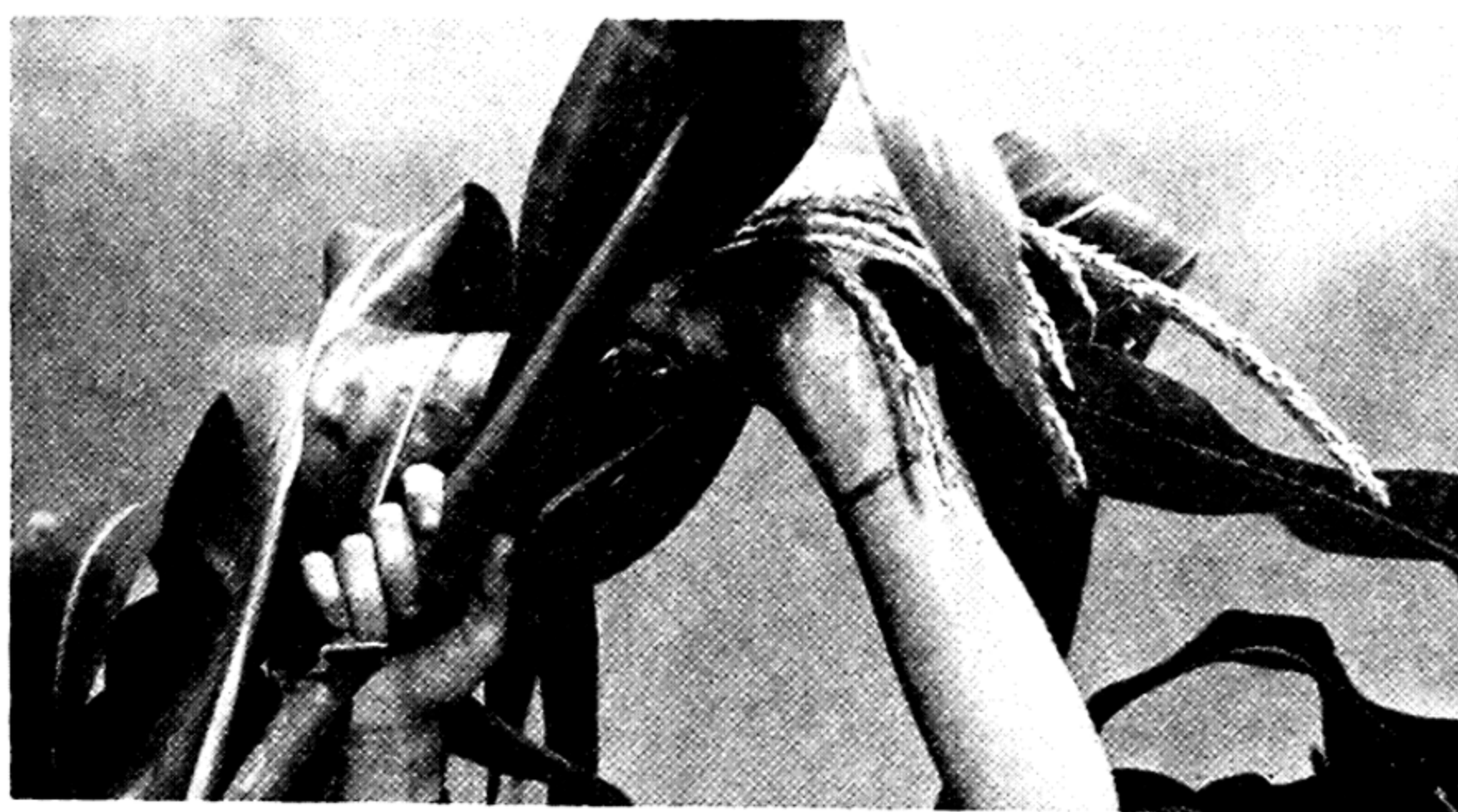


FIG. 3. The tassel is pulled by hand with a steady upward movement and dropped to the ground.

is now possible (see Chapter XIII). Cutworms and webworms may be controlled by spraying as soon as damage is noted. Wireworms, rootworms, and other insects may be controlled by soil treatment (Lilly, 1953; Lilly and Gunderson, 1953). Corn borer control by spraying is practical so that loss in yield and delayed maturity in the fall due to delay in planting can be avoided (Anonymous, 1952).

IV. Detasseling Hybrid Corn Seed Fields

Proper detasseling of the rows designated as female corn in the double-cross seed field is necessary to effect a cross mating for kernels grown on the female plants. Failure to remove the female corn tassels prior to shedding pollen, once silks have emerged on the female corn ear shoots, may result in inbreeding followed by a 25 to 33 per cent reduction in yield of the progeny (Kiesselbach, 1930; Neal, 1935; Gacitua, 1946; Airy, 1950), as compared with yield of the single-cross and, in the case of Airy, the double-cross seed.

Detasseling is started as soon as the tassel has emerged so it can be grasped by hand (Fig. 3), usually when the lower branches begin to spread, just showing above the leaves, but prior to emergence of silks

in the female plants. With some lines the tassel may remain in a leaf roll, making it necessary to open the leaves to remove the tassel. The tassel is removed by a steady upward pull and is dropped to the ground. It emerges and can be pulled one to three days before the silks emerge on the same plant, this period being reduced by adverse growing conditions, especially heat or drought. Plants differ in date of tassel emergence in areas within a field, even within a hill, so that workers must examine all plants in a field on successive days and remove tassels that are ready to pull. Immature tassels pull easily, but mature spreading tassels become "set" and hard to pull. The detasseling season is from five to ten days for any one field, depending upon uniformity of soil fertility and weather conditions.

Once silks begin to emerge on the female plants, the percentage of the plants in the female rows with shedding tassels must be kept below established maximum levels for the balance of the season. With some crosses the plant produces sucker stalks, which develop tassels and shed pollen long after the ears on the main plants have been pollinated. Sucker stalks must be removed or must be detasseled until fertilization in the female corn is completed.

Unfortunately, corn grows rapidly when the weather is rainy and warm, with the result that the number of tassels to pull per day may be greatest when field conditions for the workers are least favorable. Sunday work is often necessary.

1. Three Methods—Crew, Contract, and Machine

All detasseling is done by removing the tassel from the plant by hand. The worker walks between the rows detasseling one or two rows, depending upon (1) the percentage of the tassels to be removed that day, and (2) the size and reliability of the worker. Methods of detasseling differ in the arrangement for the supervision of the crews and in whether the worker walks through the field or rides between the rows on a machine.

a. Crew Detasseling. With crew detasseling the workers are recruited and report to the plant or to a selected location to be transported to the fields. A crew of 25 to 30 is convenient to transport and can be supervised effectively. A foreman directs the crew, instructs them on work to be done, and is in general charge. He is responsible for payroll records, for accident emergencies, and for employer responsibilities. The checker, or assistant foreman, aids in the instruction of the workers, particularly the new workers, and checks through different rows in the field to make certain that the worker understands what is wanted and to be sure that each worker is doing satisfactory work.

b. Contract Detasseling. With contract detasseling the number of acres to be detasseled by the worker is agreed upon, and a specific area within the field is assigned and marked. The contractor furnishes his own transportation and detassels only his area. He, or she, finds it best to begin detasseling a field earlier than is done with crews, removing a small percentage of the tassels each day for a period of several days rather than delay or skip days and have the "heavy pull." The earnings per hour worked usually exceed the wage rate paid to detassellers in crews, often by 25 to 30 per cent.

The contract method allows for personal initiative of the detasseler much like piecework in factories. He is told when to begin detasseling,



FIG. 4. The detasseling machine is used to transport the workers, usually 6, who pull the tassel by hand.

and the field must pass inspection every day until the job is completed. If the contract detasseler "gets behind" so that the quality of detasseling may be unsatisfactory, the producer detassels the area with a crew, charging the cost to the contractor.

c. Detasseling by Machine. The so-called detasseling machine (Fig. 4) is only a method of transporting the workers. The detasseler rides on the machine and pulls each tassel the same as if on foot. The machine is usually three wheeled with power and steering on the single front wheel. It has an overhead framework high enough to pass over the corn plant without breaking stalks. Platforms, about 18 inches wide and 3 feet long, are so located that they travel in the space between rows, providing a place for the worker to stand. A crew of six detassellers and one driver on a machine may detassel 25 to 40 seed field acres per day if not over 40 per cent of the tassels are pulled.

When a large percentage of the tassels are to be pulled, 30 per cent

or more, it is generally believed that 6 persons riding on a machine can "pull" as many tassels as 9 to 12 people traveling afoot. When the corn is quite tall or when the temperature and humidity are high, the ratio in favor of the machine may be higher.

Some producers do all detasseling with machine crews. It is more common for a producer to have enough machines to use machine crews to pull 50 to 70 per cent of the tassels in most fields. Foot crews are used to go into fields (1) before a heavy pull is possible, (2) on days when the field is not being detasseled by machine, and (3) when fields are being finished and the pull is light.

2. Quality Standards in Detasseling

Quality standards used by all producers cannot be readily determined. The author has some knowledge of practices followed by producers of both certified and noncertified seed. Only a few instances are known where practices followed by private brand producers are less strict than the certification standards; more instances are known where the opposite applies.

It is common to detassel seed fields so that (1) the percentage of female plants with tassels shedding pollen at any one time never exceeds 1 per cent; (2) the accumulated percentage of the tassels shedding pollen for any three successive inspection dates does not exceed 2 per cent; and (3) the percentage of shedding tassels does not exceed 2 per cent in any one field, even though several fields of a hybrid combination are being grown in the same area. A tassel is regarded as a shedding tassel when the central spike or any branch has as much as 1 inch of the tassel showing emerged anthers. Under actual field conditions the percentage of effective pollination from female pollen may be much lower than the percentage of shedding female corn tassels indicates, when this definition of a shedding tassel is observed (Gacitua, 1946; Airy, 1950).

Thompson and Hutchcroft (1951) analyzed field inspection records on certified hybrid corn seed fields in Iowa in 1945 and proposed a sampling system for inspection purposes based on sequential principles as contrasted with previous practice of counting a predetermined number (usually 5) of 100-plant samples per field. In using the method, the field unit should be according to corn maturity based on planting date or soil fertility rather than according to existing fence lines or the outside boundaries of the area planted to seed corn. Another consideration is the need to sample the separate areas detasseled by individual contractors, rather than to depend on a wholly random sample as would

be appropriate in a uniform field not containing 5 to 20 contracted areas. Thompson and Hutchcroft's analysis was with inspection data from fields that were detasseled mostly by crews.

3. Personnel Organization for Detasseling

Personnel organization followed in the detasseling work is difficult to outline. The work methods differ according to the acreage to be detasseled, the number of machines available for each 1000 acres, the extent of use of contract labor, and the producer. The following is presented as a general outline.

A production unit of 2000 acres may be divided into four areas of 500 acres each, with an area supervisor assigned an area prior to planting time and through detasseling. If the detasseling is done by crews, each area man is given four or five crews of 25 to 40 each, depending upon the height of the corn, the stand in the fields, the prevailing temperatures, and the number of acres in each field or the number of fields involved. The area man then transfers these crews from field to field as required for proper detasseling of his area. Crews are transferred between areas only by the plant manager and with the agreement of the area supervisors involved. With machines available each area may require three to five machines and two crews.

Where contract workers are used, they may be assigned a specific acreage in each area. The contractors are directed by a contract-worker foreman responsible to the area supervisor. Contract workers are assigned from 4 to 7 gross acres, depending upon their physical ability, their experience, and their desires.

4. Cost of Detasseling

It is difficult to obtain actual cost figures in connection with detasseling. The cost of detasseling varies greatly according to the height of the corn; the average stand in the field; the presence or absence of sucker stalks; the physiological characteristics of the female parent variety, such as rolling of leaves around the tassel or ease of pulling the tassel; the weather which prevails during detasseling; the extent of use of machines; the age and quality of available workers; the practice of the producer with respect to pulling leaves; and the rate of pay to the laborer.

In a general way, producers in the Corn Belt have a detasseling cost of \$15 to \$40 per total acre in the seed field. The reader should recognize that there is a wide variation in actual cost of detasseling, depending upon applicable factors.

5. *Effect of Leaf Pulling on Yield*

A number of experiments have been conducted to study the effect of removal of the top leaves on the yield of the single-cross parent (Dungan and Woodworth, 1939; Borgeson, 1943; Kiesselbach, 1945; Airy, 1950). Experiments on leaf pulling in detasseling summarized by Airy (1950) are given in Table I.

TABLE I

SUMMARY OF THE EFFECTS OF DETASSELING ON YIELD WITH AND WITHOUT LOSS OF LEAVES

<i>No. of leaves removed</i>	<i>Illinois¹ per plant per cent yield</i>	<i>Minnesota² per acre per cent yield</i>	<i>Nebraska³ per acre per cent yield</i>	<i>DeKalb⁴ tests per cent yield</i>	<i>Pioneer⁵ tests per cent yield</i>
0 ^a	98	—	102	—	100
0	100	100	100	100	100
1	91	97	98	104	97
2	84	91	96	92	93
4	70	—	—	84	86

^a Not detasseled.

¹ Illinois—1938 results. Reported by Dungan and Woodworth (1939).

² Minnesota—averages for six hybrids tested in 1941 and 1942 and five hybrids in 1940. Reported by Borgeson (1943).

³ Nebraska—1944 results. Reported by Kiesselbach (1945).

⁴ DeKalb Agricultural Association. Data represents 12 varieties in 15 plots for 1944, 1945, and 1946. Reported by Harold Wright (unpublished).

⁵ Pioneer Hi-Bred Corn Company. Data from two test plots in 1944 and one in 1945. Reported by George Huey (unpublished).

Excessive leaf pulling results in reduction of grain yield. Reduction of detasseling cost, as a direct result of excessive leaf pulling, may prove to be poor economy. The reduction in yield from removing leaves with the tassel was lowest when good stands prevailed, when there was ample moisture, and when ideal corn-growing weather occurred. Borgeson (1943) states that yield reduction with early varieties was greater than with late varieties. This was due, perhaps, to a combination of stand and plant size so that the leaf area per acre was much lower with the early variety.

6. *Cytoplasmic Male Sterility*

The use of cytoplasmic male sterility, a new method of seed corn production, would make it possible to eliminate or to reduce the labor required for detasseling. The method, now being used in a limited way, requires a mixture of seed produced by the male-sterile seed stock with seed produced in the normal manner to assure pollination in the farmer's double-cross field of feeding corn.

Complete adoption of the cytoplasmic male-sterile technique now available would make detasseling unnecessary on two-thirds of the acreage.

Under present plans the seed field is planted with a ratio of two-thirds of the female corn planted to the male-sterile single cross, requiring no detasseling, and one-third of the female corn planted to the normal single cross, which requires detasseling. It is assumed the seed field blend must provide 25 to 33 per cent normal plants to assure pollination in the farmer's field. More experience is needed to be certain the field blend provides enough normal plants in all kernel sizes. Unpublished data for a hybrid seed field in 1952 with seed samples from adjacent normal and tassel sterile female rows show the following percentages of normal-type seed in each size with a 2-to-1 blend of sterile and normal types and with equal yield assumed: LF, 44; MF, 32; MF-1, 24; SF, 23; LR, 44; MR, 35; MR-1, 30; and SR, 25, instead of 33 for each size. Details on cytoplasmic sterility are given in Chapter V. Some lines can be made sterile, and still others are variable as to sterility, depending upon soil fertility, weather, and length of day.

The cytoplasmic male-sterile method is now being used in a limited way by a number of producers. A few are using the method extensively. Standards have been set up in the certification program with respect to cytoplasmic sterile seed stock production, its increase, and the certification of the cytoplasmic male-sterile double cross. The hybrid number is the same for certified seed produced by normal or by cytoplasmic male-sterile methods. Yield tests are not conclusive that the new method gives the farmer higher yields. General opinion is that the yield level of the double cross is about the same (Jones, 1953). Greater expenditures for corn-breeding research and seed stock production will be required; thus, there is little, if any, net saving in cost to the producer. The very difficult problem of detasseling will be simplified.

Research is in progress to identify and test male pollen restorers so that seed fields could be produced without the use of the normal corn in a blend, without detasseling, and with all of the progeny plants that would shed pollen in the farmer's field. This pollen restoration method holds much promise but is not in commercial practice to date.

V. Seed Corn Harvest—Field and Plant Operations

For simplification this discussion is based on a typical seed corn plant operation. Figure 5 gives a diagram outline of seed corn plant operations. There are variations, however, not only among different producers but also in the practice of single producers with plants in dif-

ferent geographical areas. For instance, harvesting, drying, and shelling may be done at one location, with the sizing, cleaning, and storage done elsewhere; or all operations may be done in one plant.

An aerial photograph of a seed corn plant located at Algona, Iowa, is shown (Fig. 6).

Harvest season—picking seed fields, husking, sorting, and drying—ordinarily begins when the corn has about 35 per cent moisture content, about September 20 in Iowa, and ends at about 20 per cent mois-

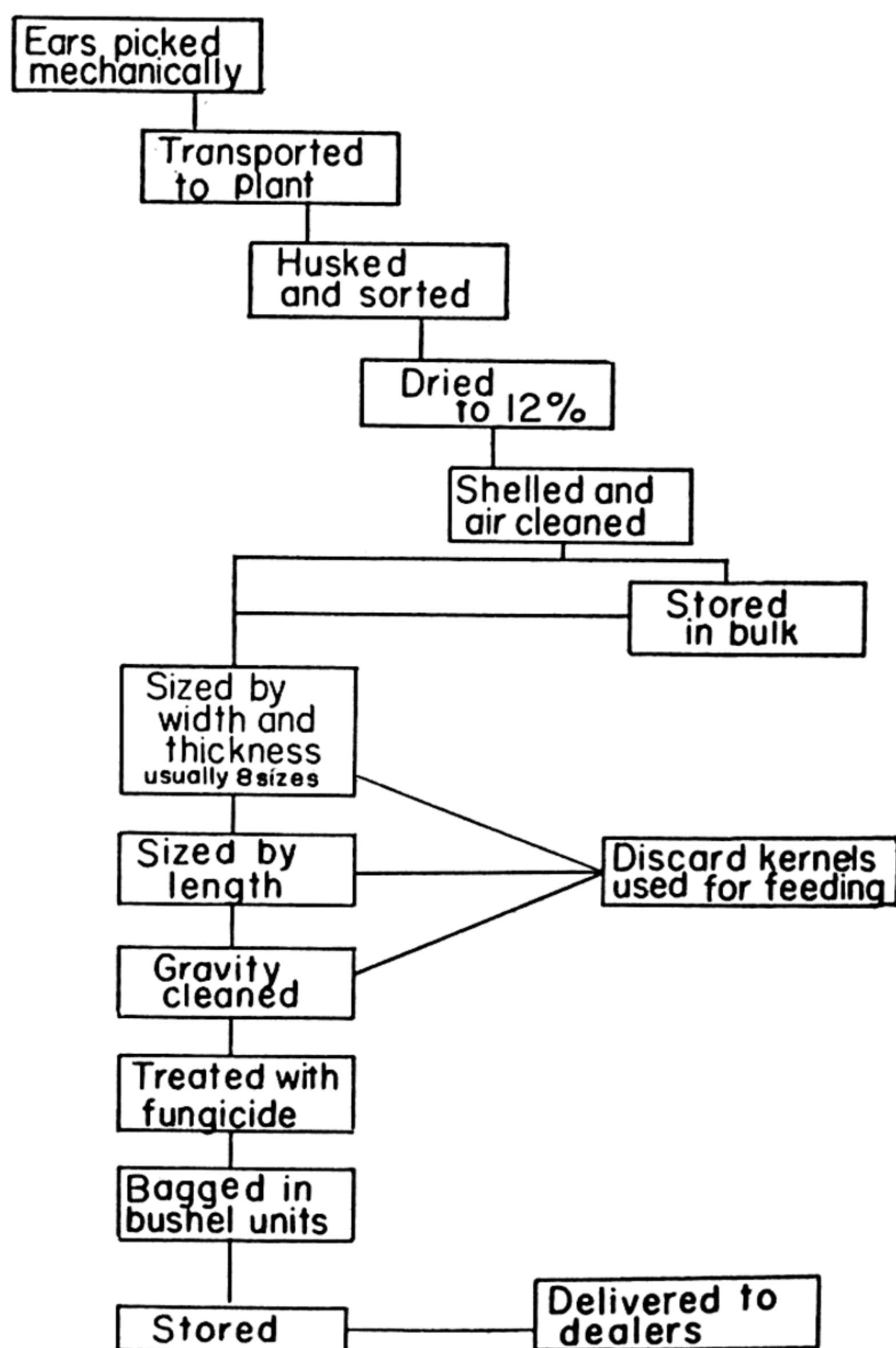


FIG. 5. Harvest and plant operations at a typical hybrid corn seed plant.

ture content five to six weeks later, about October 25 to November 1. Shelling, sizing, cleaning, treating, etc., are discussed separately, even though these operations may begin as soon as the first bin is dry.

Harvest rate ranges from 3000 to 6000 bu. of corn per day from the field, with a mean of about 3800 bu. in a plant with drying bin capacity of 22,000 bu. and drier capacity of 250,000 cubic feet of heated air per minute. Once bins are full, this requires handling the product at this rate each day through all the operations. Sizing may be at a lower

rate, with the balance of the shelled corn stored in bulk or in bags to be sized later.

The daily harvest of 3600 bu. of corn with 30 per cent moisture content is equivalent to about 160 tons of incoming product per day. The drying system removes about 70,000 pounds (35 tons) of water per day. For each 100 bu. of incoming ear corn, about 15 bu. is lost in (1) sorting, (2) handling loss at conveyor head pulleys, (3) shattering of shelled corn, (4) wet shelled corn removed by huskers, (5) drying, since grain is purchased on No. 3 or No. 4 grade basis and dried to 12

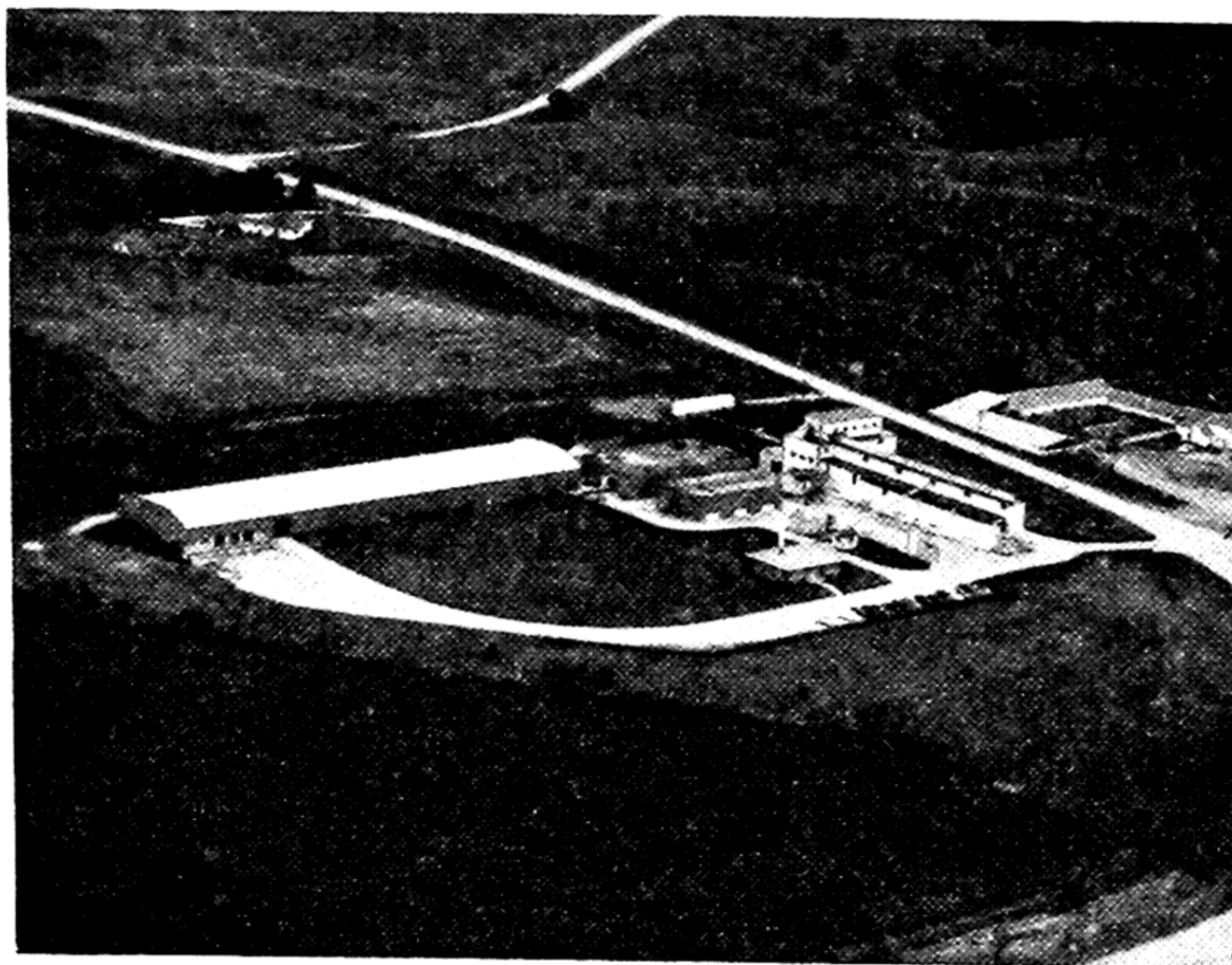


FIG. 6. A modern seed corn production plant located at Algona, Iowa.

per cent moisture, and (6) an item of 2 to 4 per cent that cannot be accounted for. This unaccountable item is, apparently, overestimate of bushels delivered from the field as compared with dry shelled grain obtained from the same bushels after drying.

1. When to Begin Harvesting Seed Corn

Harvest of seed corn begins as soon as the crop is physiologically mature. Hybrids of varying maturity are planted within a plant area, with early hybrids harvested first to get operations started and later hybrids harvested in order of maturity, early to late. Thus a majority of the seed crop may be harvested at 35 to 25 per cent moisture level owing to the later maturity of succeeding hybrids. Very dry weather in the autumn or an early killing frost may stop growth and lead to lower than normal moisture levels at harvest.

If corn is immature, as with the crops in 1945 and 1951, the risk of freeze injury is very great, and harvest may be started at 40 to 45 per cent moisture content in the grain. Disadvantages are recognized, but

seed harvested at 40 to 45 per cent moisture, even though immature, with no freeze injury to viability is likely to be more productive than seed harvested after freeze injury with resultant 5 to 50 per cent reduction in viability. Such immature corn may never mature normally owing to killing frost at normal dates. Immature or high-moisture corn seed is susceptible to severe freeze injury throughout the harvest period unless unusual drying weather prevails.

Early harvest as at 30 per cent moisture (1) avoids excessive loss of seed in the field due to mechanical picker, (2) reduces risk of delays in harvest due to rainy weather, (3) reduces risk of abnormally low temperatures prior to completion of harvest of all seed, (4) prevents further development of ear rot fungi (Hoppe, 1953), (5) stops insect damage, such as corn borer and corn-ear worm, and (6) avoids severe shelling losses due to machine picking and plant handling of seed harvested at 15 to 22 per cent moisture content. The current expense for fuel and power to dry mature corn is not excessive compared with the possible losses. Gains in seed resistance to mechanical damage are small after seed is about 30 per cent moisture content (Kaerwer, 1953). Thus in the Corn Belt it seems the seed crop should be harvested when the grain contains 35 to 25 per cent moisture content, regardless of calendar date.

2. *Freeze Injury to Germination*

Freeze injury to germination of seed corn is a major hazard in the Corn Belt, increasing from south to north. Shaw (1951) gives a basis for estimating hazard of low temperature levels, such as 32°F., 28°F., and 16°F. for different areas within Iowa.

Reduction in viability of corn seed from freeze injury with a given low temperature is greatest with highest moisture levels (Kiesselbach and Ratcliff, 1920; Holbert and Burlison, 1931; Dimmock, 1947; Rossman, 1949a, b; Aboul-Ela, 1952). Variables influencing amount of injury are (1) temperature, (2) variety of seed, (3) duration of exposure, (4) husk protection, (5) physiological maturity of seed, and (6) rate of drying after freezing. Rate of thawing had no significant effect on viability of the frozen corn. When seed was allowed to dry slowly after freezing, germination averaged 20.3 per cent higher than corresponding seed dried in the corn drier shortly after freezing (Rossman, 1947, 1949a,b).

Koehler *et al.* (1934) suggest it is best to pick seed corn before cold weather, regardless of stage of maturity. Since mature seed proved of greatest value, his recommendations point to the need for hybrid corn seed producers to plant seed fields in areas where chances are good that the single cross will mature prior to cold weather. Even so, harvesting

immature seed seems preferable if the choice is between freeze injury and immature seed.

3. *Corn Maturity and Seed Quality*

Physiological maturity in corn or maximum dry weight in the grain occurs at about 35 to 40 per cent moisture content in the grain (Robinson, 1934; Rather and Marston, 1940; Rossman, 1947; Dessureaux *et al.*, 1948; Shaw, 1949; Shaw and Thom, 1951; Aboul-Ela, 1952). Maximum dry weight occurred at 29.2, 35.2, and 40.0 per cent moisture content with three varieties of widely differing maturities (Shaw and Thom, 1951) given from early to late. A four-year average of these same three varieties shows maturity percentages varying from 6 to 10 per cent among years. Aboul-Ela (1952) found variation in moisture content at maximum dry weight for plants within a variety, the early plants reaching maturity at 29 per cent and the late plants at 40 per cent when the variety averaged 35.4 per cent moisture content in the grain at maturity. Also, the late crop in 1947 reached maturity at higher moisture levels than the more normal crop in 1948.

Advantages in seed quality (1) appearance of seed, (2) emergence of seedlings under adverse growing conditions, (3) resistance to mechanical injury by handling in seed corn plants, (4) reduced susceptibility to injury by drying temperatures as 110°F., and (5) increased yield with increased maturity even with equal field stands, have been reported (Tascher and Dungan, 1928; Harrison and Wright, 1929; Robinson, 1934; McRostie, 1949; Livingston, 1951; Kaerwer, 1953). Data reported are based on germination tests under favorable growing conditions or on only seed viability, except for the data of Kaerwer (1953), who reported cold test germinations.

In seasons when corn is late in maturity, early frost may check growth so that normal maturity never occurs.

In 1946 seed was harvested at three levels of moisture, over 36 per cent, 30 to 35 per cent, and under 30 per cent, and given artificial mechanical damage to study maturity and plant damage influences on cold test germination of the seed. The average cold test germination for untreated seed with no damage was 54, 64, and 77 per cent, respectively; and with artificial mechanical damage, 27, 37, and 57 per cent, respectively. Treated seed tested 92, 93, and 94 with no damage, and with damage 91, 91, and 93, respectively (unpublished data).

4. *Picking the Seed Field*

The farmer is responsible for picking the corn from the female rows and for delivering the seed to the plant. He is instructed as to the time

and rate to pick. Usually, only one hybrid is picked at a time, and all fields of a hybrid are mixed as delivered to the plant.

The two-row, mounted-type picker is commonly used so that only the female rows need be picked at high moisture. The male rows are picked later when dry enough to crib.

Mechanical damage by the picker may be reduced by driving slowly, by driving squarely on the row, by using snapping rolls that are fairly

TABLE II
NUMBER OF POUNDS OF EAR CORN OF DIFFERENT GRAIN MOISTURE LEVELS,^a
WET BASIS, EQUIVALENT TO 56 POUNDS OF GRAIN WITH 15.5 PER CENT
MOISTURE, WET BASIS^b

<i>Per cent moisture</i>		<i>Wet weight, pounds of ear corn required to yield 56 pounds (1 bu.) of shelled corn containing 15.5 per cent moisture</i>		
<i>In grain</i>	<i>In cobs</i>	<i>Grain</i>	<i>Cobs</i>	<i>Total</i>
10	8.93	52.58	10.91	63.49
15	18.63	55.67	12.22	67.89
20	32.89	59.15	14.81	73.96
25	45.26	63.09	18.16	81.25
30	52.44	67.60	20.90	88.50
35	56.62	72.80	22.91	95.71
40	59.08	78.87	24.29	103.16
45	59.98	86.04	24.84	110.88

^a Part of table by Iowa State College, Farm Crops Subsection letter October 4, 1945.

^b Based on the following assumptions:

- 1. The moisture content of kernels and cobs is equal when ear corn moisture is at 12 per cent.
- 2. The ratio of dry weight of cob to dry weight of grain is essentially constant throughout the grain moisture range 40 per cent to 10 per cent.
- 3. The shelling percentage used is 82.7—a value which will give 56 pounds of 15.5 per cent moisture grain from 65.06 pounds of 12 per cent moisture ears.

new, by having the rolls set closely together, by removing pegs from the snapping rolls or at least adjusting the number of pegs according to the cleanness of picking desired, and by releasing the ear retainer pressure on the husking rolls if they are present. Efforts are made to leave husks on the ear to minimize kernel scuffing and shelling loss. Farm-type elevators for loading trucks should be run at slow speeds.

Picker losses in the field with corn for cribbing vary from 2 to 25 per cent, with 5 per cent regarded satisfactory. Losses increase with delayed harvest date (Hull, 1950). Losses in seed fields are usually quite

low, since harvest of seed corn ends about the time picking for cribbing begins.

5. Determining Bushels Delivered from the Field

Seed corn harvest may begin when the grain has 30 to 40 per cent moisture content, requiring a method of estimating the bushels of grain from the weight of the wet ear corn. Compensation to the farmer grower

TABLE III
PERCENTAGE STANDARD ERROR^a FOR FOUR METHODS OF ESTIMATING POUNDS
OF DRY GRAIN IN BUSHELS FROM WEIGHTS OF EAR CORN
DIRECTLY FROM THE FIELD^b

Number of truck loads sampled for moisture content	Methods			
	A	B	F	H
1	1.8	5.2	4.0	5.4
2	1.2	3.6	3.0	4.7
3	1.0	3.0	2.6	4.5
4	0.9	2.5	2.4	4.4
5	0.8	2.3	2.3	4.3
10	0.6	1.6	2.0	4.2
15	0.5	1.3	2.0	4.1
20	0.4	1.1	1.9	4.1

^a Plus and minus 2 times standard error is random variation based on odds of 1 in 20 or times 1.66 is the range with odds of 1 in 10.

^b Only four of the methods reported by Kempthorne *et al.* (1948) are shown here.

Description of methods:

A—Directly estimating by furnace drying the sample; one sample from every truck.

B—Directly estimating by furnace drying the sample; one sample from each of a sample of trucks.

F—Estimating moisture content with one sample from each of a sample of trucks and shelling percentage with one sample from one truck. (Similar to family of curves suggested by Schmidt, 1948.)

H—Estimating moisture content in kernels with one sample from each of a sample of trucks. (Similar to use of a standard curve as given in Table II.)

is based on equivalent bushels of No. 2, No. 3, or No. 4 shelled corn, averaging 15.5, 16.5, and 17.5 per cent moisture content, respectively.

Conversion tables have been issued by the state agricultural colleges, but they are not in agreement. The Iowa table, a portion of which is given in Table II, was reissued as a Farm Crops Subsection letter on October 4, 1945. A modification for reducing error caused by seasonal and area influence on actual shelling percentage is suggested (Schmidt, 1948). Kempthorne *et al.* (1948) studied the error of estimate for different sampling frequencies and methods, a part of which is given in Table III. It is clear, (1) that the lowest error of estimate was with Method A, taking a sample from every truck, drying the sample, and

calculating the equivalent bushels of shelled corn; and (2) that the error was greatest with Method H, essentially the same as a conversion table based on only shelled corn moisture content, as in Table II. Errors of estimate apply to the grower but are compensating to a producer with many growers. Most producers find the actual bushels of shelled corn obtained after drying is 2 to 5 per cent less than the estimate of bushels harvested.

6. Unloading, Sampling, Husking, and Sorting

As the wagons or trucks of corn are unloaded at the plant, samples are taken for determining (1) the moisture of the corn, (2) the percentage of husks for husk deduction, and (3) the bushels delivered. Samples must be taken in a random manner and for use (3) should include both shelled grain and ears. Sample frequency must take into account variation of product throughout the day as well as within the field. Sample size must be adequate.

Husking seed corn within plants is done by a number of different makes and arrangements of huskers. The typical husking and sorting arrangement provides for a flow of corn over the huskers onto a wide sorting conveyor belt. The sorting conveyor may be from 18 inches to 60 inches wide, with a belt speed of 35 to 40 f.p.m. Provision is made for returning unhusked ears to the huskers, disposing of off-type or moldy ears into discard corn conveyors, and disposing of husks that are removed by hand, and there is an arrangement at the end of the belt for removing shelled corn so that only kernels attached to the cob go to the drying bins for use as seed. Speed to operate the huskers and the angle of decline with the rolls are largely controlled by the design of the husking machine and the roll. Rubber rolls are most common.

The sorting operation is usually limited to removal of entire ears from the flow of ear corn. Sorters are trained to recognize and are instructed to remove male corn ears, ears that are off-type, perhaps largely volunteer corn, ears that are infected with *Fusarium moniliforme*, *Diplodia zeae*, *Gibberella zeae*, *Nigrospora oryzae*, and ears that are off color or mixed in color. The corn, as it leaves the sorting belts, is nearly free of husks, silks, and shelled corn.

Sometimes field husking and sorting units are set up at the farm. As the picker wagons are unloaded, the corn is run over the husking bed, sorted by four to six workers, and run directly into the truck for delivery to the drying bins at the seed corn plant. In this case the husks, shelled corn, and discard ear corn are left on the farm to be used by the farmer. Thus this discard corn and corn shelled by the picker do not enter into the cash payment.

Another method is for the corn to be unloaded directly to the husking and sorting belts at the plant, with husks, shelled corn, discard corn, and refuse accumulated in a bin and returned to the farmer. Thus, again, the cash payment to the farmer is on the basis of sorted ear corn.

7. Drying the Seed Corn

The first hybrid corn seed drier in the Corn Belt was built and used at Johnston, Iowa, in 1926. It was a metal-type grain bin with a subfloor built about 18 inches above the bottom. The subfloor was screened to allow air to pass through the chamber under the false floor, up through the corn, and out the top of the bin. A bin drier was also used in Wisconsin in 1926 for open-pollinated varieties of seed corn (Wright and Duffee, 1927) and had been used previously for drying feed corn.

The Wisconsin system of bin drying ear corn, using heated forced air, was developed for seed corn producers in Wisconsin during the period of 1926 to 1932. Many variations of these early bin drying arrangements are in use. The Campbell Heating Company, Des Moines, Iowa, designed drying systems for many Corn Belt producers and have supplied a large number of furnaces for seed corn drying. A co-operative project between the Campbell firm and the Pioneer Hi-Bred Corn Company led to the development of the "portable drier" in 1935. The portable drier is an oil- or gas-fired furnace and fan built into a metal housing and mounted on a truck chassis. The portable feature permits moving the source of heated air along the building to the desired bin, substituting for air ducts in the building, thus allowing lower investment in building and equipment as compared with a stationary furnace and air ducts and resulting in reduced fire risk.

Drying the seed is a major part of plant operations. It requires a large investment in drying bins, burners or driers, and conveying equipment for filling and emptying bins. All other operations are planned according to plant drying capacity. Drying practices differ, but the most common is to dry the corn on the ear until about 12 per cent in moisture content. A few seed corn plants are designed so that the ear corn is dried to about 18 per cent moisture, with the drying of the shelled corn completed in a shelled corn drier. The seed is dried to the same moisture content, but the improved drying efficiency of the shelled corn drier is used to remove the last 5 to 6 per cent of moisture.

Unpublished data show that the percentage of cold test germination for untreated seed shelled at different moisture levels was 18 per cent, 87; 16 per cent, 91; 14 per cent, 92; 12 per cent, 91; and 11 per cent, 94. Apparently, most producers have found injury to the germination

from shelling at higher moisture levels and prefer to dry the corn to 12 per cent on the ear before shelling.

Figure 7 illustrates a drying building with a stationary furnace for simplicity. The corn is usually 8 to 10 feet deep, and the air flows through two bins or two depths of corn. Basic design is to blow in through two partly dry bins and exhaust through one high-moisture bin, giving low air velocity on the partly dry corn and high air velocity on the high-moisture corn. With portable driers the bin floors slope to a lower center tunnel with the driers moved along the outside and connected to the bin by means of a canvas duct.

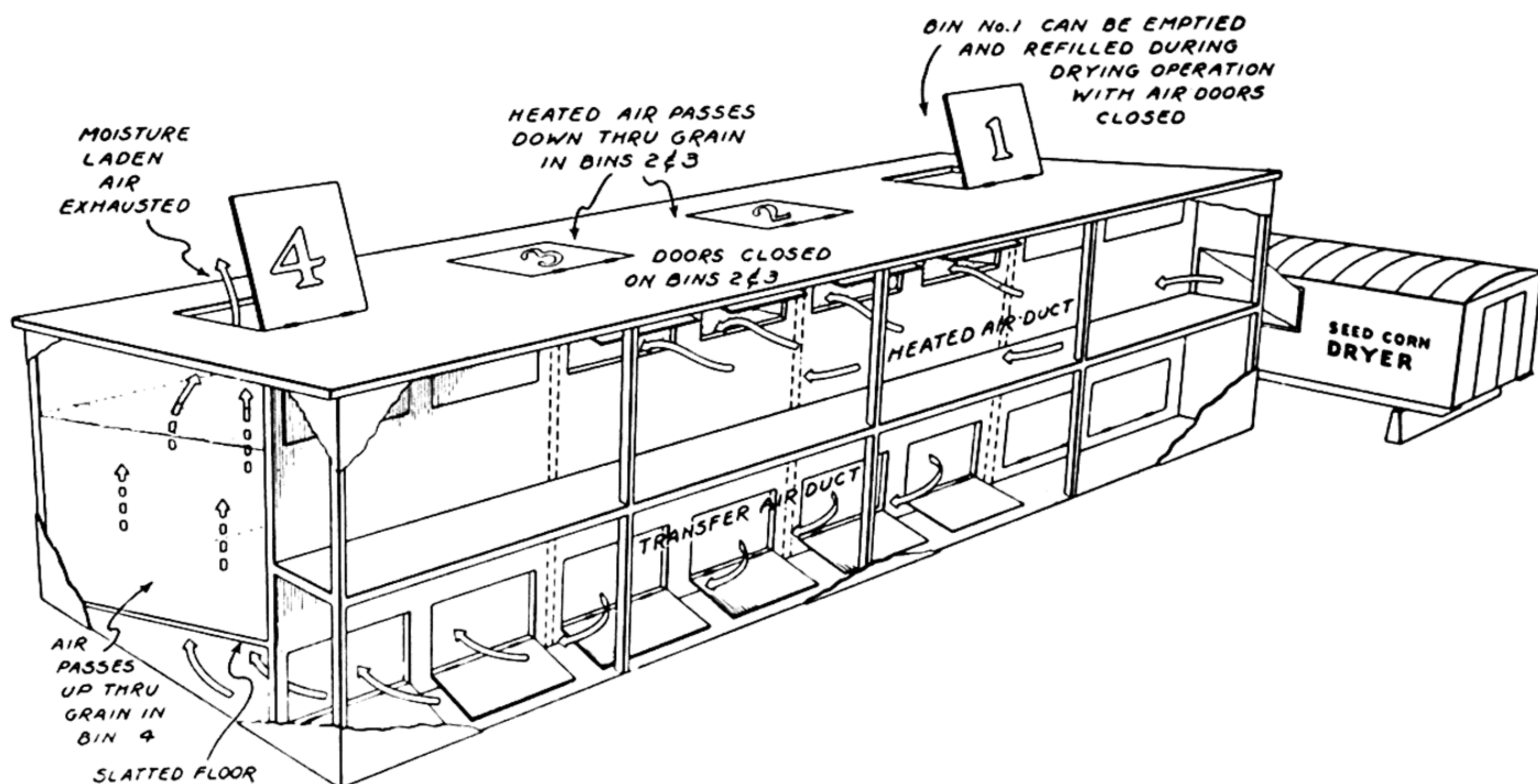


FIG. 7. Diagram illustrating principles used in both bin arrangement and air flow in a seed corn drier.

Fuel with portable driers may be fuel oil or natural, propane, or butane gas. Coal furnaces and steam boilers require large investments and are not common.

Air volume is based on 13 cubic feet per minute per bushel with air velocities through the bin of 50 cubic feet per square foot of bin area with partly dry corn and 100 cubic feet per square foot of bin area with high-moisture corn. Static pressure is low, about 1.25 to 1.50 inches of water under the first bin.

The multivane slow-speed fan with forward-curved blades was used until about 1950 when the backward-curved blade came into favor. The latter type is nonoverloading on the motor (Madison, 1949; Henderson and Perry, 1952) and delivers more constant air volume with changes in static pressure due to corn depth.

Drying temperatures of 105° to 120°F. are reported noninjurious to seed viability (Harrison and Wright, 1929; Robinson, 1934; Royer,

1935; Kiesselbach, 1939; Wileman and Ulstrup, 1945; Dimmock, 1947; McRostie, 1949). Seed with initial high moisture content is more susceptible to injury with high temperatures and may best be dried at 105° to 110°F. (Royer, 1935; Wileman and Ulstrup, 1945; McRostie, 1949). Rapid drying at noninjurious temperatures did not cause injury (Robinson, 1934; Koehler and Dungan, 1940) except with frozen corn (McRostie, 1949). Desiccation with unarmful temperatures to moisture levels of 4 per cent (Harrison and Wright, 1929), 6 per cent (Dungan, 1924), 3 per cent (Bryan, 1953), and 2 per cent (Dimmock, 1947) did not injure viability but did retard emergence and seedling vigor (Dimmock, 1947). Tatum (1942) found, however, evidence of increased mechanical damage in commercial seed lots with reduced moisture content as from 12 to 8 per cent. The above are with tests evaluating seed injury by viability, greenhouse germinations, field stands, and field yield tests, all rather favorable conditions.

Experiments to determine effects of drying temperatures on both warm test and cold test germinations were conducted in 1941 and 1942 (unpublished data). The results are summarized in Table IV. There

TABLE IV

SUMMARY OF COLD TEST GERMINATION RESPONSE OF NOT TREATED SEED HARVESTED AT DIFFERENT MOISTURE LEVELS AND DRIED AT DIFFERENT AIR TEMPERATURES, EXPERIMENTAL DRIER SIZE 8 CUBIC FEET PER BIN WITH PLUS AND MINUS 2°F. THERMOSTATIC TEMPERATURE CONTROLS. DATA ARE AVERAGE OF 3 HYBRIDS IN EACH RUN. WARM TEST GERMINATION, VIABILITY, NOT AFFECTED SIGNIFICANTLY

Year	Run	Average moisture content	Air dry	Percentage cold test germination ^a (hours to dry in italics)			
				95°	105°	110°	115°
1941	1	36.6	30 days	150	119	103	86
			91	88	85	79	68
			Air dry	95°	95°-105° 110° ¹	95° 115° ²	95°-105° 115° ³
	2	34.7	30 days	131	98	87	88
			92	93	92	90	91
	3	27.5	30 days	82	59	55	43
			92	90	90	90	87
1942	1	32.2	95	89	88	90	87
	2	30.5	90	85	84	84	83

^a Note because of variation in cold test germinations on different dates only comparisons of temperature levels within a run are valid.

¹ Temperature increased to 105° at 37 hours and to 110° at 61 hours, both after start of drying.

² Temperature increased to 115° after 37 hours of drying.

³ Temperature increased to 105° at 37 hours and to 115° at 61 hours, both after start of drying.

was a consistent reduction in seed strength as measured by cold test germination for increasing drying temperatures with seed viability reduced only at highest temperature levels in 1942.

Air temperatures of 115°F. may be used when moisture content is 20 per cent or less, when the seed was mature prior to harvest, and when the single cross is not susceptible to injury by high drying temperatures. The margin of safety may be small in the 115°F. temperature range. Drying temperatures of 100° to 105°F. seem necessary to avoid injury to high-moisture corn. The lower air temperature on wet corn may give improved cold test germination only with adequate air volume to prevent uneven drying. Drying temperatures in the range of 105° to 110°F. seem unharmed in most instances.

VI. Shelling, Sizing, and Cleaning

Shelling, sizing, and cleaning of seed corn are all operations to prepare a uniform, high-quality product, satisfactory in appearance and easily planted by the farmer customer in existing equipment.

Each operation results in loss or removal of corn. Common seed production experience is for the bushels of shelled corn to be about 85 per cent of the bushels delivered by the grower. The total bushels of all salable sizes of seed with 12 per cent moisture content is usually 65 to 75 per cent of the bushels of No. 3 corn delivered from the field. The ratio of bushels of sized seed to bushels of shelled corn ranges from 78 to 88 per cent. Estimates of normal cleaning and sizing loss are: air cleanings—1 per cent; tips (below $1\frac{7}{64}$ round-hole screen)—4 per cent; short kernels removed—9 per cent; and gravity machine rejections—3 per cent; all vary according to influences of lots, hybrids, growing area, and seasons.

1. *Shelling the Seed Corn*

The cylinder sheller is generally used for shelling seed corn, owing to its convenience and high capacity. Shellers have been modified, using special rubber coverings on the cylinder with enlarged cylinder cages to maintain shelling volume per hour and still give low reduction in cold test. Special rubber-covered, cone-type shellers have been built. Certain models of commercial shellers are operated at reduced cylinder speeds.

Tests to measure sheller damage by cold test germination were conducted in 1939 (unpublished data). Four plant cylinder shellers were compared with hand-shelling with the following cold test germination

percentages for not treated seed listed in order of cylinder- versus hand-shelled: Plant A, 66, 88; Plant B, 75, 91; Plant C, 54, 80; and, Plant D, 70, 92. A spring sheller at Plant D gave 82 per cent compared with the cylinder sheller at 70 per cent. Later tests with a rubber-covered, double-cone type sheller gave the following results: hand-shelled, 86; hand-type spring sheller, 85; and, rubber-covered sheller, 76; all are cold test germination percentages for not treated seed.

Extensive studies in 1945 (unpublished data) show the following cold test germinations for four methods of shelling: (1) hand-shelling, (2) with a one-hole hand spring sheller, (3) with a plant spring sheller, and (4) with a plant cylinder sheller. Percentages for untreated seed were 77, 71, 71, and 63, and for treated seed 86, 81, 80, and 77, respectively. A plant spring sheller operated at speeds of 205, 315, and 425 r.p.m. gave seed with cold test germinations of 77, 74, and 68, respectively.

A cylinder sheller operated at speeds of 240, 360, 480, 600, and 720 r.p.m., in 1944 (unpublished data) gave cold test germinations of 74, 66, 61, 59, and 50, for untreated seed, and 79, 79, 77, 79, and 64, for treated seed, with both given in order of increasing sheller speed.

2. Sizing and Cleaning the Shelled Corn

Dividing shelled corn into sizes according to width, thickness, and length of kernel is herein referred to as sizing. Frequently, the terms "grade" and "grading" are improperly used to denote sizing. In reference to other products "grade" more commonly denotes quality rather than variation in size dimensions; different sizes of kernels do not consistently vary in productivity and thus are not of a different "grade."

The shelled corn is first cleaned, using either a special aspirating machine or an air cleaner in conjunction with shaker screens for sizing divisions. The sizing operation divides the kernels into groups according to width and thickness. Two basic methods of sizing are used. (1) The thickness division may be made first, using different widths of slot screen, and then the different components divided with round-hole screens within the slot screen divisions, according to width of the kernel (Table V); (2) The round-hole screens may be used first, dividing the corn according to width of kernel (round-hole screen. Table VI). The usual practice is to reject both the extra large kernels passing over $2\frac{5}{64}$ round-hole screen and the extra small kernels passing through a $1\frac{7}{64}$ round-hole screen and then make four divisions. The four components from the round-hole separations are divided or sized with slot screens, according to thickness of kernel. The kernels passing through

TABLE V

OUTLINE OF SCREEN ARRANGEMENT FOR SIZING CORN SEED, USING SLOT SCREENS
FIRST AND THEN DIVIDING EACH PORTION WITH DIFFERENT
ROUND HOLE SCREENS
Screen sizes given in 64ths of an inch

<i>Slotted screen</i>	<i>Round-hole screen</i>	<i>Length sized</i>	<i>Gravity^b cleaned</i>
Over 14	LR—Large Round 22–25	No	Yes
	LR—Large Round 20–22	Yes	Yes
	MR—Medium Round 18–20	Yes	Yes
	SR—Small Round 17–18	Yes	Yes
Through 14 Over 13	TF—Large Thick Flat 22–25	Yes	Yes
	TF—Medium Thick Flat 20–22	Yes	Yes
	Thick Flat Discard Through 20		
Through 13 Over 12	LF6—Large Flat 22–24	Yes ^a	Yes
	MF6—Medium Flat 20–22	Yes ^a	Yes
	MF5—Medium Flat 18–20	Yes	Yes
	Small Flat Discard 17–18		
Through 12	MF4—Medium Flat 18–20	Yes	Yes
	SF—Small Flat 17–18 or 17½–18½	Yes	Yes
	Tips—Discard 16–17		

^a Short kernels reworked and used as special size only if needed.
^b Discard from gravity cleaner used for feed only.

TABLE VI

OUTLINE OF SCREEN ARRANGEMENT FOR SIZING CORN SEED, USING ROUND HOLE SCREENS FIRST AND THEN DIVIDING EACH PORTION WITH SLOTTED HOLE SCREENS
Screen sizes given in 64ths of an inch

<i>Round-hole screen^a</i>	<i>Slotted-hole screen</i>	<i>Length sized</i>	<i>Gravity^b cleaned</i>
Extra large Over 24 or 25	Discarded for feed		
Large Over 21, 21.5, or 22 Through 24 or 25	LR—Large Round Over 13.5 or 14	No	Yes
	LF—Large Flat Through 13.5 or 14	Yes ^c	Yes
Medium Over 18, 18.5, or 19 Through 21, 21.5, or 22	MR—Medium Round Over 13 or 13.5	Yes ^c	Yes
	MF—Medium Flat Through 13 or 13.5	Yes ^c	As needed
Medium—1 Over 17.5 or 18 Through 18, 18.5, or 19	MR—Medium Round—1 Over 12.5 or 13	Yes	Yes
	MF—Medium Flat—1 Through 12.5 or 13	Yes	As needed
Small Over 17 or 17.5 Through 17.5 or 18	SR—Small Round Over 12 slot	Yes	Yes
	SF—Small Flat Through 12	Yes	Yes
Extra small or tips Through 17 or 17.5	Discarded for feed		

^a Screen size selected to produce sizes to plant on a given plate for each size as in Table VII.

^b Discard from gravity cleaner used for feeding purposes only.

^c Short kernels reworked and used as a special size only if needed.

the slot screen are named “flat,” and those passing over the slot screen are named “round.” Table VI shows a sizing plan, using this latter plan based on round hole or width separation first, intended to be illustrative and not indicative of general practice by many producers.

With either method the important consideration is to divide the corn into sizes that will plant satisfactorily and conveniently in the farmer’s planter. Unfortunately, some early day sizing plans were developed using more sizes than necessary to give planting accuracy

(Reed, 1939; Wright, 1941; and others not published). This has been confusing to the farmer and has tended to place undue emphasis on the merits of a large number of sizes, on the need for precision in sizing, on the importance of variation within a size, and on the importance of uniform appearance of length of kernel. Seed of a given seed parent, divided on the same set of screens in two seasons, may not result in sizes that plant with the same plate each year owing to the influence of kernel length on plate required. Varying the screen properly each year and using different seed parents may result in sizes that do plant accurately with a given planter plate each year.

Following division by width and thickness, each size is divided according to length of kernel. Extremely short kernels can be removed as can the extremely long ones. The division between kernels retained and kernels rejected is not accurate according to either actual length or appearance of length of kernel.

Sizing of corn for length is more important from the standpoint of appearance or "eye appeal" than with regard to planting accuracy. Actual practice leads to removal of much larger percentages than necessary for optimum planting accuracy to give uniform appearance in the final product.

Unpublished data show the following percentages of the shelled corn in different sizes for all lots of Pioneer seed produced in Iowa in the years 1948 through 1952: Large Flat, 11; Medium Flat, 37; Medium Flat-1, 24; Small Flat, 7; Large Round, 4; Medium Round, 8; Medium Round-1, 6; and Small Round, 3. Standardized planter plates required to plant each size are discussed later and are given in Table VII. The two medium flat and medium round sizes are a division of the medium size to increase uniformity of appearance, even though a mixture of the two sizes plants conveniently and accurately. Both sizes plant with planter plates usually designated for medium size flat corn by the planter manufacturers.

The gravity cleaner is used as a special cleaner of each size after screen and length separations. It operates by a combination of vibration of a sloping table and flotation by air, removing both foreign material and lightweight kernels. These lightweight kernels may be thin chaffy kernels, cracked kernels damaged during other operations, moldy kernels, light in weight, or kernels blistered by freeze damage. The gravity cleaner is effective when adjusted properly and may be used to make improvements in the warm test and cold test germination of freeze-injured seed. It has replaced hand-sorting as done by many producers in the early day. The corn removed is low in quality and of value for feed only.

TABLE VII
STANDARDIZED SEED PLATE SUGGESTIONS ACCORDING TO SIZE NAME FOR SOME DIFFERENT MAKES OF CORN PLANTERS. SCREENS USED AS IN
TABLE VI, ADJUSTED ACCORDING TO LENGTH OF KERNEL TO MAKE A SIZE WHICH PLANTS ON STANDARD PLATE

Make of planter	Size name and code letters							
	Large	Medium	Medium	Small	Large	Medium	Medium	Small
	flat LF	flat MF	flat MF 1	flat SF	round LR	round MR	round MR 1	round SR
John Deere (Horse)	Y5529B*	Y2637B*	Y2637B	Y2636B	Y5520B	Y5511B	Y5511B	Y5519B
John Deere (Tractor)	H2156B*	H694B*	H694B	H697B	H2044B	H1933B	H1933B	H2043B
McCormick	1978A	1977A	1975A	3546A	3042A	3324A	3561A	3398A
Case	P2075*	P2075	P2073	P2322	P2300	P2296	P2321	P2310
Moline	D1139(X)	D1138	D1483A	D1386A	D4044	D4044	D4043(X)	D4043
Oliver	S831	S830	S829	S1189	S1216	S1236	S1241	S1242
Allis Chalmers	300108	300106	309431	309432	302602	302609	302609	309436
Black Hawk	F348	F347	F467	F460	F491	F454	F462	F462
Hayes	XX28	XX26.5	XX25.5	XX24.5	XX28	XX26.5	XX26	XX25

* Floor plate set with groove side next to seed plate. Unless noted by asterisk all other suggestions are with floor plate set with groove side away from seed plate.
(X) Use floor plate D4265.

3. Corn Planter Plates and Their Selection

Detailed discussion of the corn planter, the plates available, and its operation cannot be given. Airy (unpublished data) presented a plan for simplified sizing, size nomenclature, and planter plate recommendations to a joint meeting of representatives of the American Seed Trade Association and representatives of the farm machinery manufacturers in January, 1948, and again to the Association in 1954. This plan is now in operation. The farmer may purchase the same seed size in different hybrids over a period of years and needs only two plate sizes in most planters (Table VII). The seed producer must adjust screen sizes as determined for each lot to (1) reduce seasonal variation in size, (2) reduce hybrid seed parent variation, (3) give a fairly constant supply of each size each year, and (4) give a final seed size that will plant with the same seed plate year after year, abnormal seasons such as 1947 excepted. The seed size name corresponds with the plate required; it is standardized according to the plates now on hand and in use by the customer and manufacturers, not standardized according to some confusing empirical fractional screen dimensions understood in part by specialists and engineers, but not necessarily consistent with the seed plate required to plant the final size.

4. Treating, Weighing, and Bagging

Sized and cleaned seed is treated with a fungicide, weighed, bagged and sealed by sewing, ready for labeling and delivery to the customer. Some seed may be stored temporarily in special bags to be treated and used at a later date. Sized seed is seldom stored in bulk because of the large number of bins required.

a. Treating the Seed. Organic fungicides containing thiram, phygon, spergon, or captan, are used with little risk of seed damage by heavy rates of treatment and with effective control of soil pathogens and some seedling diseases. The advantages of seed treatment with a fungicide are shown in data presented under other subjects, such as drying, germination, and mechanical handling, as well as in literature references given. (Also, see Chapter XII.)

Fungicides may be applied in dust or in slurry form. Rate of application varies from 0.5 to 1.0 ounce of active ingredient per bushel. The lower rate is that usually recommended by manufacturers. Slurry application, developed for seed corn by E. I. du Pont de Nemours Company, Inc., involves a mixture of fungicide in water, 1.0 pound per gallon, with 2.3 cu. cm. of the slurry distributed over 1 pound of seed to give the 0.5 ounce rate.

Machines for applying the slurry fungicide include the original by DuPont; modifications of the original marketed by Ben Gustafson and Son Manufacturing Company, Fargo, North Dakota, and Calkins Manufacturing Company, Spokane, Washington; a semiautomatic batch treater (Armer, 1948a, b); a continuous-flow treater with slurry sprayed on the seed (Kepner and Leach, 1950); a continuous-flow slurry treater without spray by Superior Grain Separator Company, Hopkins, Minnesota; a continuous-flow slurry treater without spray by Pioneer Hi-Bred Corn Company, Des Moines, Iowa; and a continuous-flow treater with fungicide, water spray, and grain introduced simultaneously into a rotating drum by Green Giant Company, Le Sueur, Minnesota.

Seed may be treated for control of grain storage pests (Cotton and Ashby, 1952). Pyrethrin powders and finely ground dust impregnated with piperonyl butoxide may be mixed with seed as a preventive. Lindane applied at 1 p.p.m., or a dust containing 3 per cent of DDT added to the seed at the rate of $\frac{1}{2}$ ounce per bushel, are described as effective control measures. No damage to seed was observed with either insecticide at recommended dosages, but Cotton does not quote tests, such as cold test germinations, or field stands with cold wet soils with treated samples tested immediately and after six months or more of storage.

Insecticides for control of soil-borne insects may be used as a seed treatment, but are seldom applied to double-cross hybrid corn seed by the seedsman (Lilly, 1953; Lilly and Gunderson, 1953; Packard, 1952). If used, they are usually applied by the customer on the farm just prior to planting. Many times, though, the insecticide is applied as a spray on the soil or as an additive mixed with either the starter or the broadcast fertilizer instead of as a seed treatment.

b. Weighing and Bagging the Seed. Seed corn is sold in 1-bu. and $\frac{1}{2}$ -bu. units. The bag most commonly used is 28-ounce Osnaburg cotton cloth, made with 32-inch cloth cut 35 inches. Special moisture-resistant paper bags have recently been used in increasing amounts.

Cloth or sewing thread or both can be treated with DDT or with pyrethrin compounds to inhibit insect infestation (Cotton and Ashby, 1952), DDT, BHC, and Chlordane were found effective in resisting penetration but cannot be used with food products.

Mechanical arrangements for filling and closing bags vary from use of small farm-type platform scales to the automatic types used in pairs so that one scale fills and weighs while the corn from the other is dropped into a bag. Sewing machines may be (1) swinging head with a counter weight, (2) rolling platform type requiring handling, or (3) belt type requiring almost no hand labor. Bags are seldom closed by other than machine sewing.

5. *Inspection and Control of Quality during Sizing and Cleaning*

Inspection work involves determination of seed quality based on sampling and sample inspection prior to drying, after drying, and both during and after sizing and cleaning. The inspection counts supply useful information to operators for adjustment of the sizing and cleaning equipment. Routine samples are checked with test screens to control accuracy in the sizing operation. Samples of the treated seed taken at regular intervals are checked for planting accuracy, for appearance of adequate treatment, and for accuracy of labeling. The statistical quality control method, adopted by industry during and following World War II, has been applied effectively to part of these inspections. It is especially adapted to the control of accuracy of bag weights.

6. *Germination Tests Indicate Seed Quality*

a. Warm Test Germination. The warm test germination measures maximum viability of seed. The test is run at about 80°F. with high relative humidity. Three common test techniques are used: (1) the kernels are wrapped in cloth or in paper towels, using the conventional rag doll test technique; (2) the kernels are placed on moist blotters; and (3) the seed is planted in sterile sand. Warm germination is the legal germination requirement and is the conventional test used in most experiments to measure seed corn quality by germination.

b. Cold Test Germination. The cold test germination is a laboratory method of simulating adverse field conditions when temperatures are low and soil is wet. Reddy (1935) reported differences in germination and growth response with *disease-free seed* planted in soil in pots but held at 40°F. temperature for varying periods preceding room temperatures. No differences occurred at room temperatures with no preceding cold temperature exposure. Raymond Baker, of Pioneer Hi-Bred Corn Company, observing Reddy's experience, attempted similar tests in a greenhouse in the fall and winter of 1935–36, and then began controlled temperature laboratory work in the winter of 1936–37. S. F. Goodsell took over this work in 1937 and improved the techniques. Iowa State Seed Laboratory developed the technique now widely used in other states (Porter and Rice, 1941, 1942). Hoppe (1951) has proposed a paper doll cold test, requiring less soil and thus less physical facilities. In all cases the biological variations in the soil used contribute to variation in test severity.

Earlier and later studies with cold resistance of plants and seedling diseases have been reported, which dealt with (1) causal organisms in

disease-infested seed, (2) causal organisms of root rot in corn, (3) effect of temperature on the disease and seedling response, and (4) plant physiological characteristics contributing to cold tolerance and plant growth (Melhus and Durrell, 1922; Dickson and Holbert, 1926; Johann *et al.*, 1928; Holbert and Burlison, 1929, 1930, 1931; Reddy, 1933; Smith, 1935; Rossman, 1949a, b).

The cold test germination has been found effective as a laboratory method correlated with field stands under cold wet soil conditions. Organisms causing reduced stands are primarily *Pythium* species (Porter and Rice, 1941; Ho, 1944; Hoppe, 1949; Hoppe and Middleton, 1950) but include other species, such as *Fusarium*, *Helminthosporium*, *Sclerotium*, *Rhizoctonia*, and *Trichoderma*. Study of cold test methods and development of and evaluation of the test at the experiment stations occurred largely from 1935 to 1945 (Reddy, 1935; Porter and Rice, 1942; Porter, 1944; Rice, 1944; Reddy and Gerhold, 1948; Neal, 1949; Isely, 1950; Hoppe, 1951).

Isely (1950) reviews development of the cold test technique and discusses the merits and limitations of the cold test method. Seed factors responsible for lowered emergence under cold test conditions are given by Isely as (1) injury to the pericarp, (2) old seed, (3) immaturity, (4) frost injury, and (5) genetic characteristics. Isely cautions that the cold test indexes are only a reflection of materials and methods used in a given laboratory and are not necessarily comparable among laboratories unless equalized by control samples. Principal applications of the cold test are given by Isely (1950) as (1) evaluation of corn seed lots as to merchantableness of carry-over seed, (2) experimental evaluation of seed-protectant chemicals (both beneficial and harmful effects), (3) evaluation of procedures in seed corn plants that may influence cold test germination of corn, and (4) evaluation of differences between inbred lines and hybrids in regard to cold resistance. Isely (1950) points out limitations of the test as being in the area of labeling requirements or in buyers' specifications because of difficulty in standardization of the test even within a given laboratory, especially among laboratories.

Haskell and Singleton (1949) found good correlations for greenhouse cold tests and field stands, but point out limitations of the cold room test. Unpublished data from a well-standardized laboratory, running several thousand tests per year, show the validity of comparisons of germination of different lots within tests, but show the limitations of regarding cold test germinations as an empirical index of germinability of the seed for comparison of seed lots germinated in different tests.

In conducting the test, samples of corn seed grain, either treated or

not treated with a fungicide, are laid in a soil medium; the trays are first held in a high-humidity cold chamber, usually about 50°F. for six to ten days; the trays are moved to a conventional warm germination chamber with 80°F. and high humidity. Seed rot is given a chance to develop in the cold room, with the extent of damage determined by the percentage of seed still viable. Most laboratories make early field plantings at several dates each spring (often during April) for correlation of cold test results with early field stands. Such studies give a basis for evaluating the practical limits of the differences in cold test germination obtained in the laboratory in terms of field stands.

Work with open-pollinated seed corn found reduction in germination, seedling vigor, and yield from broken and damaged seed planted in field conditions (Brown, 1920; Melhus and Durrell, 1922; Meyers, 1924; Alberts, 1927). Melhus and Durrell (1922) and Alberts (1927) observed that saprophytic fungi invaded the seed through breaks in the pericarp with inhibiting influences on germinability and growth. Tatum (1942), Tatum and Zuber (1943), Airy (1947), Neal (1949), Pinnell (1949), Wortman and Rinke (1951), Rush and Neal (1951), Rinke (1953), and Kaerwer (1953) studied the cold test and its merit as a method for evaluating seed strength of hybrid corn seed under cold wet soil conditions and studied plant procedures contributing to reduced cold test germination.

c. Tetrazolium Stain for Estimating Viability. Injury to viability may occur when seed corn is subjected to field temperatures below 30° to 32°F. A quick method of estimating the germinability after freeze is suggested by Lakon (1942), using differences in stain reaction for viable and nonviable seeds in the presence of tetrazolium salt. Porter *et al.* (1947), Goodsell (1948), and Bennett and Loomis (1949) report studies using Lakon's method on maize seeds and conclude that significant correlations exist between stain reaction and germinability of corn seed injured by freeze. The method is not critical but provides an estimate of extent of injury from freeze within a few hours.

7. Storage and Handling of Bagged Seed

The main requirement for storage space for seed corn is that it be dry, free of rodents, and free of grain storage insects. Seed corn in bushel bags is adapted to the use of pallets and the fork truck for transporting and piling pallets of corn. Figure 8 illustrates a pallet of corn being put into the warehouse with a fork truck. Such mechanical handling is being adopted by some of the larger producers as a substitute for seasonal labor.

Shelled corn may be bagged for storage until sized. Bulk handling

and storage must be done with care to avoid mechanical damage. Also, corrective ventilation fan systems may be needed to prevent moisture transfer within the grain unless outside temperatures are not lower than grain temperature (Hukill, 1953).

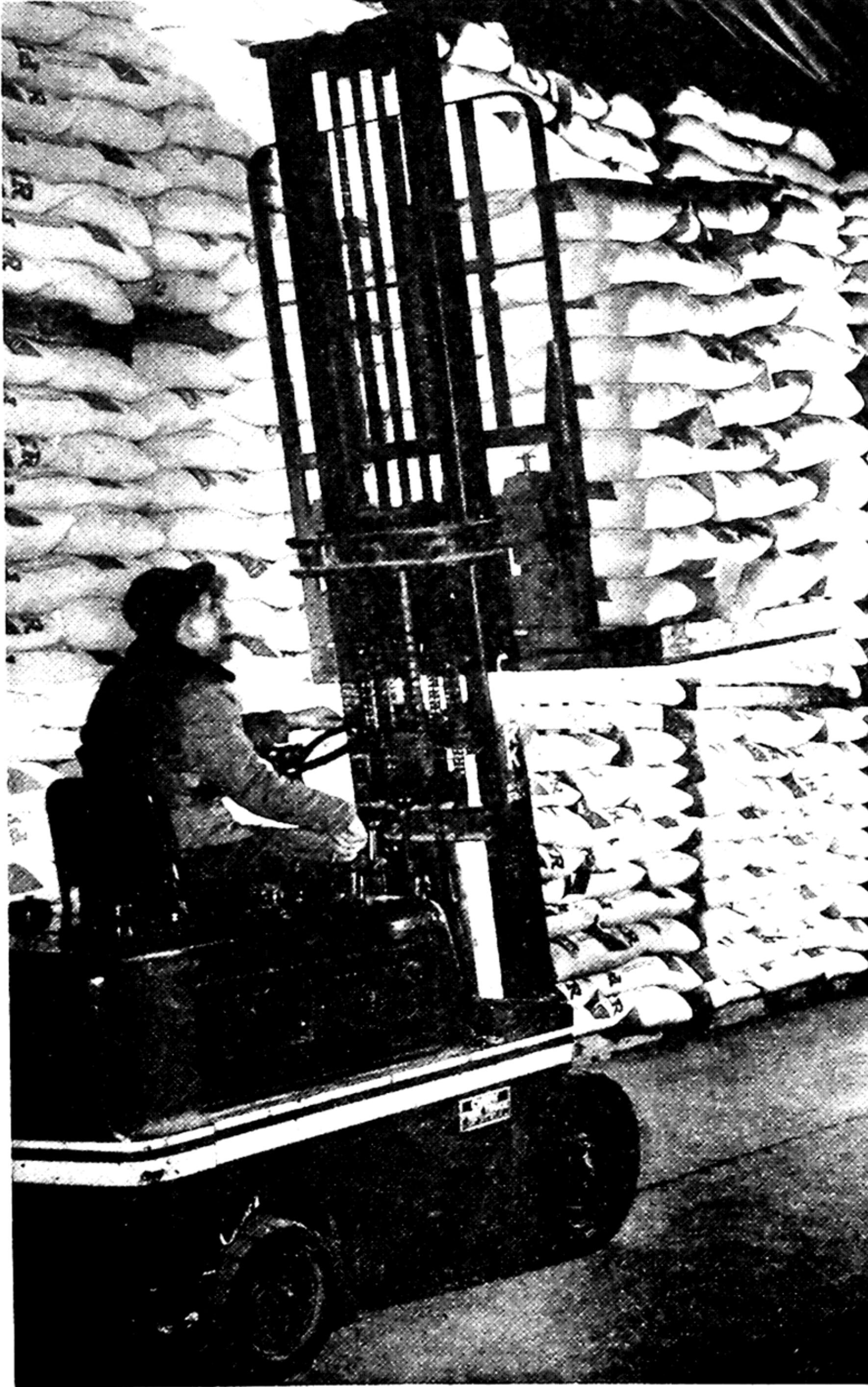


FIG. 8. The fork truck and pallet handling 72 bu. of seed corn is used to transport bags to the warehouse and stack them.

Seed corn is stored in bags in unheated warehouses with no damage to warm test or cold test germination from low winter temperatures if the grain is as dry as 12 per cent. No damage to corn in lower bags seems to occur even though the bags are piled 16 feet high. Adequate protection against moisture must be provided to keep the bottom layer

of bags from absorbing moisture, largely condensation on the cement floor on certain days during the spring months.

8. Storage of Surplus Seed

The supply of seed corn a producer has for delivery in any year is affected directly by the yield level in that year. Pioneer seed field yields in Iowa for each of ten years from 1944 through 1953 were: 70.0, 58.0, 78.5, 44.1, 80.1, 70.3, 63.7, 66.4, 90.4, and 80.7 bu., respectively, delivered per female corn acre. The yield in 1952 was more than double that in 1947. Estimates when planning acres of seed fields to be planted are based on normal yields. Large seasonal variations in yield cause an oversupply of seed in some years and a short supply in others so that surplus seed corn of any size should be held at least until the quantity and quality of the succeeding crop is known. The customer often prefers one-year-old seed when the new crop is of doubtful quality because of drought, immaturity in a slow season, or freeze injury prior to completing harvest.

Storage of single-cross and inbred seed for many years is desirable. Tests reported by Sayre (1948) and a five-year test conducted co-operatively by American Can Company and Pioneer Hi-Bred Corn Company from 1948 to 1953 (unpublished data) show the influence of reduced storage temperature and reduced moisture level in the grain on increased longevity of viability, field stand germination, and cold test germination. Low temperature was of greatest influence in maintaining germinability when moisture levels were 11 per cent or lower.

Surplus double-cross seed requires only one year of storage (one summer) before it can be planted. Such seed should not be used unless it is satisfactory for delivery to the customer and should not be blended with new crop seed under any circumstances. Tests with seed stored through one summer under different conditions, such as 0°F., 34°F., 50°F., uncooled plant warehouses, show little difference in cold test, except that lower cold test germination occurred with seed stored in plant warehouses at normal temperatures (unpublished data). Reductions in cold test germinations of 5 to 25 per cent occurred in plant warehouses with not treated seed. The loss was greatest with seed with initial low cold test, and the loss was not entirely recovered by treatment with a fungicide.

Air-conditioning engineers suggest that a warehouse, being cooled to 50°F. in the Corn Belt, should have the equivalent of 2 inches of cork insulation on the sidewalls, 3 inches on the ceiling, and a vapor barrier seal to give a reasonable investment in cooling equipment and low operating costs. A review of studies of moisture equilibrium content by

Bailey (1921), Coleman and Fellows (1925), Alberts (1926), Barre (1938), Stahl (1948), Brockington *et al.* (1949), and Theimer (1951) shows that for dent corn about 12 per cent moisture is the equilibrium moisture content with an atmosphere containing 50 to 60 per cent relative humidity. Henderson and Perry (1952) show minor influences by temperature level on this balance.

VII. Sales and Distribution Methods

There are two common methods used for seed corn sales and distribution in the Corn Belt: (1) sale through dealers from stocks in the dealer's store, and (2) direct sales to the farmer. The dealer method is commonly used in the merchandising of farm seeds. With the introduction of hybrid corn many farmer customers were skeptical of its merit and were slow to buy it from the dealer. This led to the development of the direct sales method. The corn company engages salesmen in various communities to explain the new product and to solicit business by farm-to-farm sales.

1. Dealer Sales Method

The dealer sales method is used for many other crop seeds, such as alfalfa, clover, soybeans, etc. Some companies who have used the dealer or store sale method with other crop seeds added hybrid corn seed. Sales depend largely upon the activity of the local dealer in combination with the general advertising done by the producer. The arrangements with dealers differ, but it is customary for the dealer to purchase the corn and stock it for resale. The dealer or store sales method is especially adapted to new areas where the competition is not great, or where the total volume of corn is not large enough to justify farm-to-farm calls by a salesman.

2. Direct Sales Method

The direct sales method depends on the use of local salesmen to (1) call on the farmer, (2) solicit his business, (3) write up an order, (4) receive corn in the spring on consignment, (5) arrange for the customer to pick up the corn at the salesman's place of business or some other designated location, (6) complete the actual sale and collect for the corn when the farmer receives it, and (7) give service to the customer as is needed throughout the growing season. The salesman is paid a commission based on bushels sold. In some companies the sales supervisors receive commissions as an incentive to greater sales effort, whereas in other companies the sales supervision is paid by salary, partly to avoid undue sales pressure.

In a direct sales method the company carries responsibility for the entire sales program, including payment of regional advertising in magazines, on radio, and television; co-operation in the payment of local advertising; and consignment of the corn to the salesman.

REFERENCES

- ABOUL-ELA, M. M. 1952. Physiological changes and freezing injury in maturing maize. *Plant Physiol.* **27**: 778-786.
- AIRY, J. M. 1947. Factors affecting stand. *Rept. Second Ann. Hybrid Corn Industry-Research Conf.*, pp. 6-10.
- AIRY, J. M. 1950. Current problems of detasseling. *Rept. Fifth Ann. Hybrid Corn Industry-Research Conf.*, pp. 7-17.
- ALBERTS, H. W. 1926. Moisture content of corn in relation to humidity and temperature of atmosphere. *J. Am. Soc. Agron.* **18**: 1029-1034.
- ALBERTS, H. W. 1927. Effect of pericarp injury on moisture absorption, fungus attack, and vitality of corn. *J. Am. Soc. Agron.* **19**: 1021-1030.
- ANONYMOUS. 1952. The European corn borer and its control in the north central states. *Iowa Agr. Expt. Sta. Pamphlet* **176**.
- ANONYMOUS. 1953. Hybrids continue advance throughout the country. United States Department of Agriculture, Bureau of Agricultural Economics. Mimeograph release July 13, 1953.
- ARMER, A. 1948a. A mechanical spray treater for sugar beet seed. *Proc. Fifth General Meeting Am. Soc. Sugar Beet Technol.*, p. 108.
- ARMER, A. 1948b. Spreckels will treat all seed issued to growers. *Spreckels-Sugar Beet Bull.* **xii**: 11-12.
- BAILEY, C. H. 1921. Respiration of shelled corn. *Univ. Minnesota Agr. Expt. Sta. Tech. Bull.* **3**.
- BARRE, H. J. 1938. Vapor pressure in moisture transfer. *Agr. Eng.* **14**: 247-249.
- BENNETT, N., and LOOMIS, W. E. 1949. Tetrazolium chloride as a test reagent for freezing injury of seed corn. *Plant Physiol.* **24**: 162-174.
- BORGESON, C. 1943. Methods of detasseling and yield of hybrid seed corn. *J. Am. Soc. Agron.* **35**: 919-922.
- BROCKINGTON, S. F., DORIN, H. C., and HOWERTON, H. K. 1949. Hygroscopic equilibria of whole kernel corn. *Cereal Chem.* **26**: 166-173.
- BROWN, E. B. 1920. Relative yields from broken and entire kernels of seed corn. *J. Am. Soc. Agron.* **12**: 196-197.
- BRYAN, A. M. 1953. Determination of moisture in seeds. Ph.D. thesis, Iowa State College, Ames, Iowa.
- COLEMAN, D. A., and FELLOWS, H. C. 1925. Hygroscopic moisture of cereal grains and flaxseed exposed to atmospheres of different relative humidities. *Cereal Chem.* **2**: 275-287.
- COTTON, R. T., and ASHBY, W. 1952. Insect pests of stored grains and seed. *Yearbook Agr. U. S. Dept. Agr.*, pp. 629-639.
- DESSUREAUX, L., NEAL, N. P., and BRINK, R. A. 1948. Maturation in corn. *J. Am. Soc. Agron.* **40**: 733-745.
- DICKSON, J. G., and HOLBERT, J. R. 1926. The influence of temperature upon the metabolism and expression of disease resistance in selfed lines of corn. *J. Am. Soc. Agron.* **18**: 314-322.
- DIMMOCK, F. 1947. The effects of immaturity and artificial drying upon the quality of seed corn. *Can. Dept. Agr. Tech. Bull.* **58**.

- DUNGAN, G. H. 1924. Some factors affecting the water absorption and germination of seed corn. *J. Am. Soc. Agron.* **16**: 473-481.
- DUNGAN, G. H. 1944. Yield and bushel weight of corn grain as influenced by time of planting. *J. Am. Soc. Agron.* **36**: 166-170.
- DUNGAN, G. H., and WOODWORTH, C. M. 1939. Loss resulting from pulling leaves with the tassels in detasseling corn. *J. Am. Soc. Agron.* **31**: 872-875.
- DYAS, E. S., BODENSTEINER, L. J., and ANDERSON, M. A. 1952. How to grow corn. *Iowa Farm Sci.* **6**: 151-153.
- GACITUA, H. L. R. 1946. Factors which determine the importance of contamination in corn. M.S. thesis, Iowa State College, Ames, Iowa.
- GOODSELL, S. F. 1948. Triphenyltetrazolium chloride for viability determination of frozen seed corn. *J. Am. Soc. Agron.* **40**: 432-442.
- HARRISON, C. M., and WRIGHT, A. H. 1929. Seed corn drying experiments. *J. Am. Soc. Agron.* **21**: 994-1000.
- HASKELL, G., and SINGLETON, W. R. 1949. Use of controlled low temperature in evaluating the cold hardiness of inbred and hybrid maize. *J. Am. Soc. Agron.* **41**: 34-40.
- HENDERSON, S. M., and PERRY, R. L. 1952. "Engineering Elements of Agricultural Processing." Edwards Brothers, Inc., Ann Arbor, Michigan.
- HO, W. 1944. Soil inhabiting fungi attacking the roots of maize. *Iowa Agr. Expt. Sta. Research Bull.* **332**.
- HOLBERT, J. R., and BURLISON, W. L. 1929. Studies of cold resistance and susceptibility in corn. *Phytopathology* **19**: 105-106.
- HOLBERT, J. R., and BURLISON, W. L. 1930. Cold resistance and susceptibility in corn. *Phytopathology* **20**: 117-118.
- HOLBERT, J. R., and BURLISON, W. L. 1931. Cold resistance in corn. *J. Am. Soc. Agron.* **23**: 1061.
- HOPPE, P. E. 1949. Differences in *Pythium* injury to corn seedlings at high and low soil temperatures. *Phytopathology* **39**: 77-84.
- HOPPE, P. E. 1951. A new technique for incubating seed corn in cold soil for disease tests. *Phytopathology* **41**: 747-751.
- HOPPE, P. E. 1953. Infections of corn seedlings. *Yearbook Agr. U. S. Dept. Agr.*, pp. 377-380.
- HOPPE, P. E., and MIDDLETON, J. T. 1950. Pathogenicity and occurrence in Wisconsin of *Pythium* species which cause seedling disease in corn. Abstract in *Phytopathology* **40**: 13.
- HUKILL, W. V. 1953. Grain cooling by air. *Agr. Eng.* **34**: 456-458.
- HULL, D. O. 1950. *Iowa State Coll. Agr. Ext. Serv. Pamphlet* **161**.
- ISLEY, D. 1950. The cold test for corn. *Tiré à part des Compt. rend. assoc. intern. essais semences* **16**: (No. 2). Copenhagen V.
- JENKINS, M. T. 1936. Corn improvement. *Yearbook Agr. U. S. Dept. Agr.*, pp. 455-522.
- JOHANN, H., HOLBERT, J. R., and DICKSON, J. G. 1928. A *Pythium* seedling blight and root rot of dent corn. *J. Agr. Research* **37**: 443-464.
- JONES, D. F. 1953. Progress report on male sterility. *Rept. Eighth Ann. Hybrid Corn Industry-Research Conf.*, pp. 7-10.
- JONES, M. D., and BROOKS, J. S. 1950. Effectiveness of distance and border rows in preventing outcrossing in corn. *Oklahoma Agr. Expt. Sta. Tech. Bull.* **T-38**.
- JONES, M. D., and BROOKS, J. S. 1952. Effect of tree barriers on outcrossing in corn. *Oklahoma Agr. Expt. Sta. Tech. Bull.* **T-45**.

- KAERWER, H. E., JR. 1953. Maturity in relation to seedling vigor. *Rept. Eighth Annual Hybrid Corn Industry-Research Conf.*, pp. 59-68.
- KATZ, Y. H. 1952. The relationship between heat unit accumulation and the planting and harvesting of canning peas. *J. Am. Soc. Agron.* **44**: 74-78.
- KEMPTHORNE, I. L., SCHMIDT, J. L., and SNEDECOR, G. W. 1948. The estimation of yield of corn of standard moisture content in hybrid seed corn production. *J. Am. Soc. Agron.* **40**: 645-654.
- KEPNER, R. A., and LEACH, L. D. 1950. New spray-type seed treater. *Calif. Agr.* **4**: 3-10.
- KIESSELBACH, T. A. 1930. The use of advanced generation hybrids as parents of double cross seed corn. *J. Am. Soc. Agron.* **22**: 614-626.
- KIESSELBACH, T. A. 1939. Effect of artificial drying upon the germination of seed corn. *J. Am. Soc. Agron.* **31**: 489-496.
- KIESSELBACH, T. A. 1945. The detasseling hazard of hybrid seed corn production. *J. Am. Soc. Agron.* **37**: 806-811.
- KIESSELBACH, T. A., and RATCLIFF, J. A. 1920. Freezing injury of seed corn. *Univ. Nebraska Agr. Expt. Sta. Research Bull.* **16**.
- KOEHLER, B., and DUNGAN, G. H. 1940. Disease infection and field performance of bin- and hanger-dried seed corn. *J. Am. Soc. Agron.* **32**: 768-781.
- KOEHLER, B., DUNGAN, G. H., and BURLISON, W. L. 1934. Maturity of seed corn in relation to yielding ability and disease infection. *J. Am. Soc. Agron.* **26**: 262-274.
- LAKON, G. 1942. Topographischer Nachweis der Keimfahigkeit der Mais durch Tetrazoliumsalze. *Ber. deut. botan. Ges.* **60**: 434-444.
- LILLY, J. H. 1953. Treatments for soil insects. *Rept. Eighth Ann. Hybrid Corn Industry-Research Conf.*, pp. 76-92.
- LILLY, J. H., and GUNDERSON, H. 1953. Insecticides . . . for soil insects. *Iowa Farm Sci.* **7**: 15-17.
- LIVINGSTON, J. E. 1951. Effect of low temperature on the germination of artificially dried seed corn. *Nebraska Agr. Expt. Sta. Research Bull.* **169**.
- MADISON, R. D. 1949. "Fan Engineering," 5th ed. Buffalo Forge Co., Buffalo, New York.
- MAGOON, C. A., and CULPEPPER, C. W. 1932. Response of sweet corn to varying temperatures from time of planting to canning maturity. *U. S. Dept. Agr. Tech. Bull.* **312**.
- MCROSTIE, G. P. 1949. Some factors influencing the artificial drying of mature grain corn. *J. Am. Soc. Agron.* **41**: 425-429.
- MELHUS, I. E., and DURRELL, L. W. 1922. Dry rot of corn. *Iowa Agr. Expt. Sta. Circ.* **78**.
- MEYERS, M. T. 1924. The influence of broken pericarp on the germination and yield of corn. *J. Am. Soc. Agron.* **16**: 540-550.
- NEAL, N. P. 1935. The decrease in yielding capacity in advanced generations of hybrid corn. *J. Am. Soc. Agron.* **27**: 666-670.
- NEAL, N. P. 1949. Breeding corn for tolerance to cold. *Rept. Fourth Ann. Hybrid Corn Industry-Research Conf.*, pp. 68-78.
- PACKARD, C. M. 1952. Cereal and forage insects. *Yearbook Agr. U. S. Dept. Agr.*, pp. 581-595.
- PINNELL, E. L. 1949. Genetic and environmental factors affecting seed corn germination at low temperatures. *J. Am. Soc. Agron.* **41**: 562-568.
- PORTER, R. H. 1944. Testing the quality of seeds for farm and garden. *Iowa Agr. Expt. Sta. Research Bull.* **334**.

- PORTER, R. H., DURRELL, M., and ROMM, H. J. 1947. The use of 2, 3, 5-Triphenyl-tetrazolium chloride as a measure of seed germinability. *Plant Physiol.* **22**: 149–159.
- PORTER, R. H., and RICE, W. N. 1941. Development of laboratory techniques for detection of seed-borne plant pathogens. *Ann. Rept. Iowa Agr. Expt. Sta., Part II*, pp. 34–35.
- PORTER, R. H., and RICE, W. N. 1942. Development of laboratory techniques for detection of seed-borne plant pathogens. *Ann. Rept. Iowa Agr. Expt. Sta., Part II*, pp. 31–32.
- RATHER, H. C., and MARSTON, A. R. 1940. A study of corn maturity. *Michigan Agr. Expt. Sta. Quart. Bull.* **22**: 278–288.
- REDDY, C. S. 1933. Resistance of dent corn to *Basisporium Gallarum* Moll. *Iowa Agr. Expt. Sta. Research Bull.* **167**.
- REDDY, C. S. 1935. Pathogenicity of *Basisporium Gallarum* to corn. *Report on agricultural research* for the year ending June 30, 1935. *Iowa Agr. Expt. Sta.*, p. 79.
- REDDY, C. S., and GERHOLD, N. R. 1948. The role of seed disinfectants in the control of diseases caused by soil inhabiting pathogens. *Iowa Agr. Expt. Sta. Ann. Rept., Part I*, pp. 184–185.
- REED, R. H. 1939. Grading hybrid seed corn for planting. *Agr. Eng.* **20**: 148–152.
- RICE, W. N. 1944. Laboratory methods which measure the germinability of seeds in an unfavorable environment. Ph.D. thesis, Iowa State College, Ames, Iowa.
- RICHEY, F. D., STRINGFIELD, G. H., and SPRAGUE, G. F. 1934. The loss in yield that may be expected from planting second generation double-crossed seed corn. *J. Am. Soc. Agron.* **26**: 196–204.
- RINKE, E. H. 1953. Cold test germinations. *Rept. Eighth Ann. Hybrid Corn Industry-Research Conf.*, pp. 54–58.
- ROBINSON, J. L. 1934. Physiologic factors affecting the germination and growth of seed corn. *Iowa Agr. Expt. Sta. Research Bull.* **176**.
- ROSSMAN, E. C. 1947. Viability and vigor of inbred and hybrid maize seed subjected to freezing temperatures. Ph.D. thesis, Iowa State College, Ames, Iowa.
- ROSSMAN, E. C. 1949a. Freezing injury of inbred and hybrid maize seed. *J. Am. Soc. Agron.* **41**: 574–583.
- ROSSMAN, E. C. 1949b. Freezing injury of maize seed. *Plant Physiol.* **24**: 627–656.
- ROYER, H. A. 1935. The temperature—moisture—germination relationships in the curing of seed corn. M.S. thesis, Iowa State College, Ames, Iowa.
- RUSH, G. E., and NEAL, N. P. 1951. The effect of maturity and other factors on stands of corn at low temperatures. *J. Am. Soc. Agron.* **43**: 112–116.
- SAYRE, J. D. 1948. Storage tests with seed corn. *Rept. Third Ann. Hybrid Corn Industry-Research Conf.*
- SCHMIDT, J. L. 1948. How to reduce ear corn bushels to bushels of shelled corn. *Agr. Eng.* **29**: 294–296.
- SHAW, R. H. 1949. Studies on corn phenology and maturity in Iowa. Ph.D. thesis, Iowa State College, Ames, Iowa.
- SHAW, R. H. 1951. You can figure your fall freeze hazard. *Farm Sci.* **6**: 25–26.
- SHAW, R. H., and THOM, H. C. S. 1951. On the phenology of field corn, silking to maturity. *J. Am. Soc. Agron.* **43**: 541–546.
- SMITH, O. F. 1935. The influence of low temperature on seedling development in two inbred lines of corn. *J. Am. Soc. Agron.* **27**: 467–479.
- SPRAGUE, G. F. 1942. Production of hybrid corn. *Iowa Agr. Expt. Sta. Bull.* **P48**.
- SPRAGUE, G. F., LILLY, J. H., and RUBIS, DAVID. 1950. Can planting dates beat borers? *Iowa Farm Sci.* **4**: 150–151.

- STAHL, B. M. 1948. Engineering data on grain storage. Agricultural Engineering Data I. American Society of Agricultural Engineering, St. Joseph, Michigan.
- TASCHER, W. R., and DUNGAN, G. H. 1928. Seedling vigor and diastatic activity of dent corn as related to composition of endosperm and stage of maturity. *J. Am. Soc. Agron.* **20**: 133-141.
- TATUM, L. A. 1942. The effect of genetic constitution and processing methods on the ability of maize seed to germinate in cold soil. Ph.D. thesis, Abstract in *Iowa State Coll. J. Sci.* **17**: 138-140.
- TATUM, L. A., and ZUBER, M. S. 1943. Germination of maize under adverse conditions. *J. Am. Soc. Agron.* **35**: 48-59.
- THEIMER, O. F. 1951. Ventilation of grain storages. *Agr. Eng.* **32**: 106-110.
- THOMPSON, D. J., and HUTCHCROFT, C. D. 1951. Accuracy of estimating the mean percentage of non-detasseled plants in double cross corn seed production fields. *J. Am. Soc. Agron.* **43**: 609-616.
- WILEMAN, R. H., and ULSTRUPP, A. J. 1945. A study of factors determining safe drying temperatures for seed corn. *Indiana Agr. Expt. Sta. Bull.* **509**.
- WORTMAN, L. S., and RINKE, E. H. 1951. Seed corn injury at various stages of processing and its effect upon cold test performance. *J. Am. Soc. Agron.* **43**: 299-305.
- WRIGHT, A. H. 1941. Seed corn grading in relation to planting. *Agr. Eng.* **22**: 18-24.
- WRIGHT, A. H., and DUFFEE, F. W. 1927. New seed corn curing equipment devised. *Wisconsin Agr. Expt. Sta. Bull.* **396**.

CHAPTER X

Popcorn

ARTHUR M. BRUNSON

I. Origin

Popcorn is peculiarly an American crop. Not only was corn of any type unknown to the civilized world before the discovery of America, but archeological remains indicate that popcorn types played an important part in the prehistoric development of corn on this continent. The history and origin of corn are considered in detail in Chapter I, but it may be mentioned in passing that the most primitive maize thus far known (Mangelsdorf and Smith, 1949a, b) was a popcorn discovered in Bat Cave in New Mexico and estimated to date back to 2500 B.C.

It is probably incidental that these early remnants were of popcorn type, and it should not be inferred that among the early Indians there was conscious selection of or preference for corn that would pop, or that popping was the principal method by which corn was prepared for use. It is certain, however, that corn was popped by the Indians before the coming of Columbus. Available evidence indicates that this practice was more prevalent among the tribes of South America and Central America than among those of North America. Prehistoric Peruvian graves have yielded pottery utensils for popping corn as well as actual specimens of the popped grains. Similar remains have also been found in Chile, where the extremely dry climate has favored almost perfect preservation. In contrast, popcorn types were much less common in the Indian tribes of North America, and there is little evidence either archeological or from the writings of the early explorers that corn was popped by the northern tribes as a common article of diet.

Erwin (1949) suggests that popcorn originated rather recently as a mutation from flint corn. The fact that archeological evidence indicates that the oldest remains of corn found are of a popcorn type would argue that evolution has been in the opposite direction, i.e., from popcorn to our present-day varieties. Also, the fact that popping ability is a quantitative character controlled by many genes would seem to make Erwin's hypothesis of the origin of popcorn by a single mutation very improbable.

II. Varieties

Although 50 or more varieties of open-pollinated popcorn have been listed at various times by seedsmen and grown in a small way by individual growers, only about half a dozen have been commercially important. The rest have been synonyms, minor variations of main varieties, or horticultural novelties.

Popcorns usually are classified into two main types: the rice corns, which have sharp pointed kernels, and the pearl corns with smooth rounded crowns. Three additional distinct types are the JAP HULLESS type with its characteristic short thick ear and long narrow kernels, the LADY FINGER type with many very small ears and profuse suckering, and the EIGHT ROW type, which is in reality a flint corn. Practically all varieties have white cobs.

Up until about 1925 WHITE RICE, JAP HULLESS, and QUEEN GOLDEN were the varieties in commercial production. In the early 1920's SOUTH AMERICAN appeared from a somewhat obscure origin in the Kansas City area and rapidly became an important variety in the southern half of the popcorn-growing area. A few years later, SUPERGOLD and its sister variety YELLOW PEARL began to be grown extensively as a somewhat earlier high-quality yellow. As a result of these two introductions QUEEN GOLDEN rapidly became obsolete as a commercial variety, and WHITE RICE lost ground rapidly in trade circles. These changes were followed by another upheaval with the introduction of successful popcorn hybrids in the early 1940's, and at the present time practically all commercial popcorn acreage is planted to hybrids.

A brief description of the few varieties that attained commercial importance before the coming of hybrids follows. Hybrids are listed in a later section.

QUEEN GOLDEN (GOLDEN QUEEN) was a hardy, late, yellow-pearl variety grown rather extensively in the early days in the southern part of the Corn Belt where the rice types do not thrive. The plants were large and vigorous, and yields were good. Popping expansion was only fair and quality mediocre even as measured by the standards of that time.

WHITE RICE was undoubtedly the most important variety of popcorn in the first quarter of this century. It is a variety of medium maturity and good yield and was grown extensively in western Iowa and in Nebraska. The white kernels have typical sharply pointed crowns. Quality was fair, and it was used largely in the manufacture of popcorn confections as well as by concession stands for fresh popcorn.

JAP HULLESS (JAP, LITTLE JAP, JAPANESE) has the highest popping expansion and best quality of any of the older open-pollinated varieties

of popcorn. It has very characteristic plant, ear, and kernel characteristics that are distinctly different from those of other varieties. The plants are rather small with a tendency to sucker; the leaf sheaths are covered with a heavy pubescence; and the tassel has a characteristic heavy central spike. The ears are very short and thick with 30 to 40 rows. The white kernels are long and slender and may have either round or pointed crowns. Popping expansion and tenderness are excellent, and the popped product is chalky white. A number of variations of the typical JAP HULLESS, including YELLOW JAP, are known. JAP HULLESS is relatively early and is adapted only to about the northern half of the Corn Belt.

SPANISH (SPANISH EIGHT ROW) is in reality a flint corn with fair popping quality. The plants are small and early and are adapted to northern areas. Popping expansion is mediocre, but the large size of the kernels and their tough texture adapted this variety well to processing, and it had a short period of popularity in the manufacture of caramel confections.

SOUTH AMERICAN (DYNAMITE, T.N.T., SOUTH AFRICAN) is a medium-late, large-kerneled yellow pearl that is said to have been introduced to the Kansas City area from Argentina about 1920. It gained rapidly in popularity because of its relatively good popping expansion and attractive kernels, and soon became an important variety in the southern part of the popcorn area. The popped kernels are large with a characteristic yellow mottling on the surface not present on other varieties.

SUPERGOLD (SUNBURST, YELLOW PEARL) was developed at the Kansas Agricultural Experiment Station in co-operation with the United States Department of Agriculture in the 1920's by mass selection for popping expansion from a collection of QUEEN GOLDEN type samples from many sources. Although during its development, selection was based almost entirely on popping expansion, it resulted in a fairly uniform type somewhat earlier than the parent material and with small tapering ears and small vitreous kernels with very good popping expansion. It rapidly gained favor after its distribution about 1930 and, largely under the name YELLOW PEARL, replaced a considerable portion of the acreage of WHITE RICE.

III. Popping Expansion

The ability to pop is the unique characteristic that distinguishes popcorn from other types of corn. The division is not clear cut, however, since many flint corns will pop fairly well and some dent corns will pop feebly under optimum conditions. Even among the popcorns there is a wide variation in the degree and completeness of popping.

Why popcorn pops has been a matter of conjecture and study from time to time for many years. Various untenable hypotheses have been advanced, such as peculiarities in the minute structure of the starch grain, a small volume of air imprisoned within the kernel, and expansion of a volatile oil contained only in popcorn. It is now universally recognized that popping is due to a steam explosion from moisture held in the starch grains when heat is properly applied. The question arises as to why dent corn which contains as high or higher a per cent of starch grains and which has the same amount of moisture will not pop. Weatherwax (1922) explains the difference in behavior on the basis of the desiccated colloidal material in which the starch grains are embedded. In the relatively soft endosperms of dent and flour corns the fragile cell walls allow the steam generated during the application of heat to leak out before enough pressure is generated to cause an explosion. In the flinty endosperms of popcorn, however, the starch grains are so tightly embedded in the strong confining structure that a high pressure is generated before it finally gives way, and a violent explosion results. No doubt the quality and elasticity of the colloidal matrix in which the starch grains are embedded are as important as the amount of this matrix in determining whether the corn pops well or poorly. During the popping process the kernels may be seen to swell to two or three times their normal size just before popping occurs. The pericarp may aid somewhat in resisting explosion until a high popping pressure is reached, but it is not the essential structure responsible for popping behavior.

When popcorn is popped it loses somewhat more in weight than can be accounted for by the original moisture in the corn passing off as steam. Carr and Ripley (1920) present a table giving the loss in weight during popping compared with the original moisture content of the corn and suggest that the additional loss may be accounted for by the release of water of constitution when the starch molecules are partly broken down under the influence of heat and pressure involved in the popping process. In addition to water formed by pyrolysis and dissipated as steam, it is probable that some loss of other compounds occurs through steam distillation.

Excellent popping ability is of the utmost importance to the popcorn trade. It is important to the vendor and manufacturer because it determines the volume of popped product he will obtain from a given amount of corn. It is equally important to the consumer because high popping volume is closely correlated with tenderness and high quality. Finally, it is important to the grower since whatever increases the popularity of his product increases the demand.

1. Method of Testing

Various methods of measuring popability have been used. A number of reports by early workers record the number or percentage of unpopped kernels from a given weight or volume of unpopped corn. Others have used the number of cups of popped corn from a given weight of unpopped corn. In recent years "popping expansion" or "popping volume" has been almost universally used. This is the ratio of the volume after popping to the volume before popping. Thus a popping expansion of 32 means that 1 pint of unpopped corn will produce 32 pints of popped corn.

This would seem to be an easy measurement to make, but the reading is influenced by many factors such as the rate of application of heat, the temperature of popping, and particularly the size and shape of containers used for measuring and the degree of packing of the popped corn. As a result, honest determinations from the same sample by several individuals with different equipment may vary by several points. In an attempt to devise a method that would give repeatable results by any one following directions, the Purdue Agricultural Experiment Station devised a simple apparatus (Fig. 1) involving a thermostatically controlled electric popper emptying into a hopper which leads to a measuring tube 4 inches in diameter. A measuring cup provides a charge of 200 c.c. (about $\frac{4}{5}$ of a cup), and the tube for the popped corn is so calibrated as to read directly in popping volume. A machine very similar to this was adopted by the National Association of Popcorn Manufacturers and the Popcorn Processors Association in 1946 (Anonymous, 1946) as the standard method of measuring popping expansion. Although it has no legal standing, as have many standards for grades of other commodities, it is now in general use by the popcorn trade, and popping expansion has come to be a definite and very important item of quality.

2. Moisture Content

One of the most important factors influencing the popping ability of a given sample of corn is its moisture content at the time of popping. Various moisture contents from 11 to 15 per cent have been recommended by various writers for optimum popping expansion. It seems probable that some of the disagreement is due to inaccuracies in measuring moisture content, particularly in the earlier work. Moisture content of grain is not an absolute value, but is the amount of hydroscopic moisture lost when the grain is dried under a given set of arbitrary conditions. The official standards for corn specify that the percentage of

moisture shall be that ascertained by the use of the water-oven method, or by any others that give equivalent results. The official standards for the small grains, on the other hand, specify the use of the air-oven method. These two methods give appreciably different results on corn

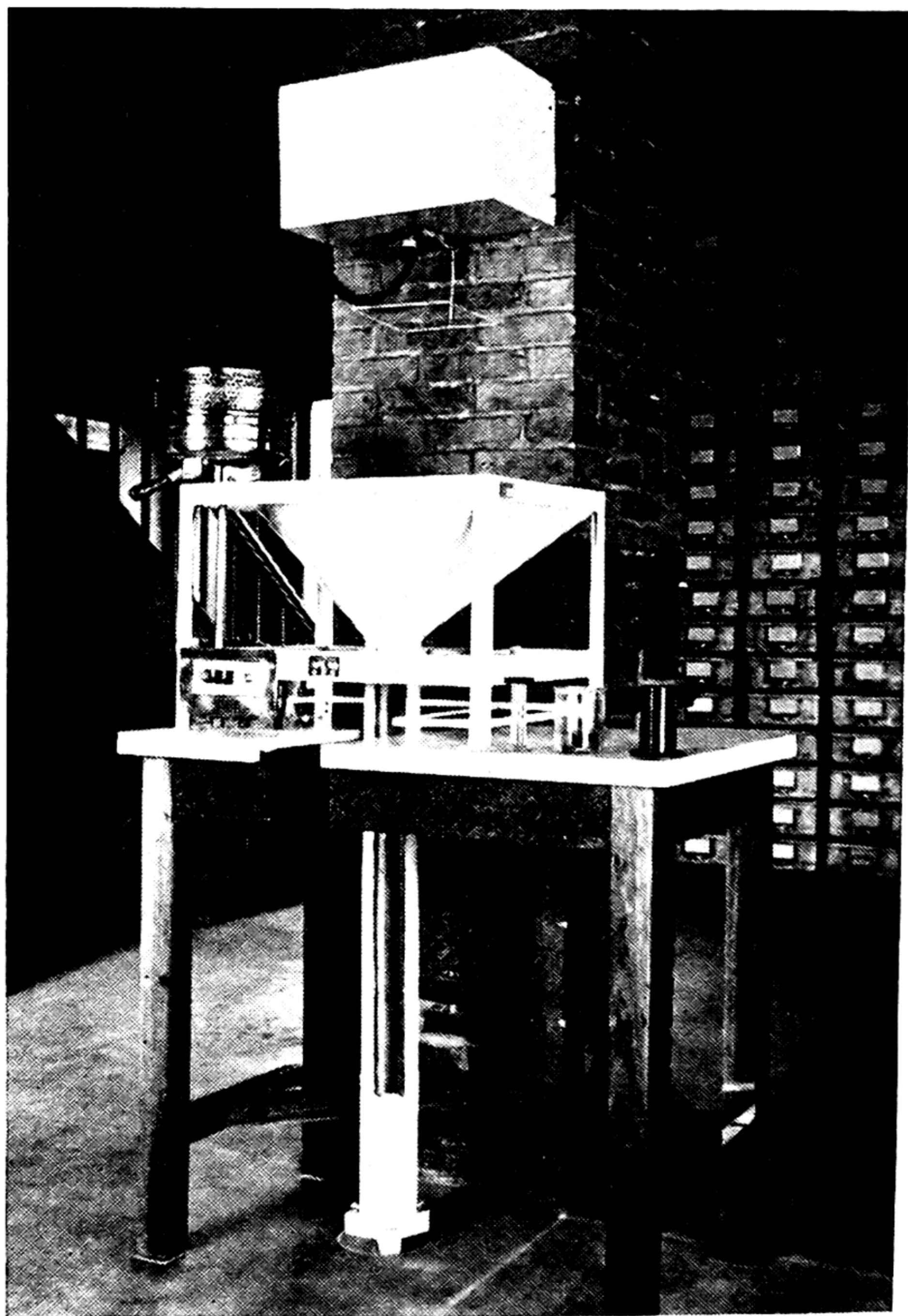


FIG. 1. Experimental popper for measurement of popping expansion of popcorn.

and cannot be used interchangeably. With the advent of electric moisture meters which are calibrated to correspond to official standards, difficulties in correct moisture determinations in popcorn have largely disappeared. The use of the Tag-Heppenstall Moisture Meters in Federal Grain Supervision Laboratories was approved in 1930. In the use of electric meters, however, care should be taken to follow directions and use the correct charts for popcorn, and in the case of the Tag-Heppenstall meter to use soybean shims instead of corn shims.

Experience indicates that about 13.5 per cent moisture is optimum for best popping when the corn is popped in seasoning or oil in an electric popper. Slightly higher moisture contents may be used to advantage when the corn is popped dry in a wire popper. Although little careful work has been done, it seems likely that the variety, the size of the kernel, and the temperature of the corn before popping may influence the optimum per cent of moisture for highest expansion. Popcorn that is too dry pops with a smooth fracture as contrasted with a very rough fracture if it is slightly too moist.

Corn with the proper moisture content pops best when heat is so applied that it starts popping in about 1 minute, and popping is completed in about 3 minutes. Most electric poppers are thermostatically controlled and adjusted at the factory for optimum temperature. Where a pyrometer is available to measure the temperature, the oil is allowed to heat to about 450°F. When the charge of popcorn is added it cools the mixture to about 330°F., which is followed by a gradual rise in temperature to about 400°F. at full popping. The cooling effect of evaporation due to release of steam during popping keeps the temperature at about this point until popping is completed.

3. Drying and Storage

In the Corn Belt popcorn seldom dries enough in the field to be in good popping condition at harvest. If picked at 20 per cent moisture or below and stored in well-ventilated cribs, it usually will reach good popping condition late in the next spring. By many, this slow curing is considered to produce the highest quality product, but the various items of storage cost are considerable. Particularly in years when there is little carry-over of old corn, there is an urgent demand to get the new crop in condition for market quickly. There have been many disappointments with artificial drying ranging from slight deterioration to total loss of popping ability. Most of these disappointments have been due to too rapid drying or uneven drying, and experienced processors now plan to dry the early part of their crop less rapidly by using forced circulation of air with little or no artificial heat. In any event popcorn should be stored on the ear until it is in good popping condition, and preferably until shortly before using.

After reaching good popping condition further changes in moisture content depend on the relative humidity and temperature of the surrounding air. Shelled corn in popping condition stored in an unheated building in the northern states during late fall, winter, and early spring will ordinarily change little in moisture content, as our average humidity is approximately in equilibrium with the moisture in the corn. Corn

stored in a heated building, however, loses moisture rather rapidly. So-called moisture-proof bags retard the loss of moisture but are not absolute insurance against going out of condition in storage for relatively long periods. Corn that has become too dry is difficult to recondition in large quantities, especially if already shelled. Water may be added if done slowly (not more than 0.5 per cent by weight at a time) accompanied by frequent mixing or transfer from one bin to another.

Storage of popcorn under refrigeration is frequently used to maintain popping condition. Eldredge *et al.* (1953) report that storage at five temperatures (-10°F. , 0°F. , 32°F. , 45°F. , and 70°F.) up to 120 days had no effect on popping volume when moisture content was held constant by sealing the corn in metal cans. Expansion of corn stored in cloth bags remained fairly constant at freezing or below but decreased somewhat at 45°F. and materially at 70°F. , where moisture content fluctuated considerably. Storage in polyethylene-lined bags inhibited moisture transfer and maintained excellent popping expansion for 120 days at temperature of 45°F. and below but allowed loss of 1.3 per cent in moisture with attendant lowering of popping volume when the popcorn was stored at 70°F. for 120 days. Apparently temperature *per se* has no effect on maintaining popping expansion, but storage under refrigeration tends to reduce moisture losses, particularly in lined bags, and hence maintains popping condition. One very real advantage of refrigeration at freezing temperature or below is the absolute control of damage by storage insects.

At temperatures of 50° to 70°F. an atmosphere with a relative humidity of 70 to 75 per cent is in equilibrium with popcorn at 13.5 per cent moisture. At lower temperatures somewhat lower relative humidities, and at higher temperatures somewhat higher relative humidities are required to maintain equilibrium. Dexter (1946) reports that popcorn stored in a tight container over a saturated solution of table salt (sodium chloride) will adjust its moisture content to 13.5 per cent over a wide range of temperatures and will hold that moisture content in the corn indefinitely. Such a storage arrangement is of value in performance trials where a series of samples is to be popped under as nearly identical conditions as possible for comparative expansion.

Since popcorn is used exclusively as human food, precautions must be taken to protect it at all times from contamination by birds, rodents, and storage insects. Officials of the Food and Drug Administration make frequent checks and may condemn as unfit for human consumption lots that are found to be contaminated. Popcorn production is under a distinct handicap in the southern states, where field infestation of the ears by the rice weevil and Angoumois grain moth is the rule.

4. *Effects of Xenia and Age on Popping*

Xenia, or the immediate effect of the pollen parent, seems to have little effect on popping expansion. Thus there is no appreciable disadvantage in popping expansion if a field of popcorn is grown adjacent to a field of dent corn so that many of the plants in the outside rows may be pollinated by a mixture of pollen from both dent corn and popcorn. Lyerly (1942) reports comparisons of popping expansion of two strains of popcorn when pollinated by dent, flint, flour, and sweet corn; seven of the eight comparisons showed slightly lower popping expansions for the outcrossed samples, averaging 1.2 points. Unreported tests from double pollinations by the author averaged even less reduction in popping expansion due to foreign pollen, although in some cases a noticeable difference in taste resulted. As Lyerly points out, xenia effect of dent corn on the *crop* is entirely different from contamination of popcorn *seed* by dent corn, which is frequently a serious item to the popcorn grower.

Good quality popcorn properly stored does not deteriorate with age. Stewart (1936) reports an experiment from which he concludes that popcorn stored on the ear pops as well after 14 years storage as at the beginning, but shelled corn lost 9 per cent of its original popping expansion in the same length of storage. The samples were stored in a cloth bag with little control of moisture content during the period. Nelson (1953) gives the results of annual popping tests from a lot of shelled corn of inbred line Sg 18 grown in 1940 and stored in friction top metal cans to prevent any change in moisture content. Over a period of 11 years no test was lower than the original; in fact, the average of the first 5 years gave a popping expansion of 32.24 and that of the last 5 years, 33.06, after a correction made for a different popper in 1950–1952. All available information indicates that popping expansion of good corn does not decline because of age if it is properly stored to protect it from storage insects and changes in moisture.

IV. Inheritance of Popping Expansion

All evidence available indicates beyond question that popping expansion is a heritable character. The variability of individual ears within an open-pollinated variety is similar to other well-known cases of quantitative inheritance controlled by many genes. A frequency distribution of 1152 ears of SUPERGOLD (Brunson, 1937) gives essentially a normal curve in which the best ears had about twice the popping expansion of the poorest ones. Significant correlations have been deter-

mined (Willier and Brunson, 1927) between popping expansion and size of kernel and proportion of soft starch, themselves quantitatively inherited characters.

1. Mass Selection

In a cross-pollinated species, a quantitatively inherited character for which there is considerable variation would be expected to be susceptible to change of its mean value under rigorous selection. The classic experiments of the Illinois Agricultural Experiment Station with their high-oil and low-oil and high-protein and low-protein strains illustrate the extreme changes that can be produced in the chemical composition of the corn kernel by this means over a period of many years.

In an experiment to test the validity of this hypothesis with popping expansion, the Kansas Agricultural Experiment Station in co-operation with the Bureau of Plant Industry of the United States Department of Agriculture started mass selection work with popcorn of the QUEEN GOLDEN type obtained from a number of sources in the early 1920's (Brunson, 1931). Each year the seed was bulked and grown in an isolated field, and in the fall between 1000 and 2000 ears were selected from agronomically good plants. These ears were numbered and popped individually during the winter, care being taken that moisture was held constant and popping conditions kept as nearly identical as possible so that the popping expansions from all ears would be comparable. From the popping expansions obtained, approximately the best 10 per cent of the ears were selected for planting the following year. After six generations of this selection the popping expansion of the strain had been increased from 19 to 26 and the variety was distributed under the name SUPERGOLD. This variety has been the source of a number of inbred lines now used in yellow hybrids.

Well-isolated plots are difficult to find in the Corn Belt, and when found are expensive and frequently inconvenient to maintain. The newer method of recurrent selection, which is essentially a refinement of mass selection using hand-pollination, is rapidly taking its place in attempts to shift the mode of quantitative characters. It seems likely that this method will be equally successful in further increasing the popping expansion of popcorn.

2. General and Specific Combining Ability

In crosses among inbred lines, two types of combining ability for quantitative characters such as yield are recognized. General combin-

ing ability means that a line behaves similarly in all crosses. Specific combining ability, on the other hand, means that an inbred line is much better than expected in some crosses and much poorer in others. These two types are not distinct or mutually exclusive, but one or the other is characteristic to a greater or lesser extent in most lines. In extensive tests at the Purdue Agricultural Experiment Station it has been found (Clary, unpublished data) that general combining ability for popping expansion is the rule but that there are occasional notable exceptions. Sg67 and SA 133 in particular gave excellent popping expansion in some combinations and very mediocre results in others.

Rather closely allied to general and specific combining ability is the relation of the popping expansion of the inbred lines themselves to that of their hybrids. Lyster (1942) reported on the popping expansion of all possible combinations among 13 yellow-pearl inbreds and among all possible combinations among 13 JAPANESE HULLESS inbreds. When the popping expansions of the parent lines are arbitrarily classified as high or low, he found that high $\times$ high gave high expansion, high $\times$ low gave intermediate expansion, and low $\times$ low gave low expansion on the average. Lyster points out that one of the JAPANESE HULLESS lines, J-2, gave rather erratic expansion data for the various crosses, presumably an illustration of specific combining ability as mentioned above.

In making up experimental dent corn double crosses the common practice is to predict the most desirable combinations from the performance of single crosses. Peterson *et al.* (1949) have shown that the same method is valid in predicting yield, standing ability, and popping expansion of three-way crosses in popcorn. Presumably it would be equally useful in predicting performance of popcorn double crosses.

V. Popcorn Hybrids

Popcorn hybrids have as much advantage over open-pollinated popcorn varieties in yield and standing ability as dent corn hybrids have over the varieties they replaced. In addition, the better popcorn hybrids produce a uniform product of appreciably higher popping expansion than previously available. It is little wonder that hybrids rapidly took over the acreage when seed became available in quantity in the early 1940's and that today practically all commercial popcorn is grown from hybrid seed. Not only has more economical production resulted to the grower from the use of hybrids, but the improved quality has greatly increased the demand from the consuming public. Annual production is shown graphically in Fig. 2, and it will be noted that although the

amounts sometimes fluctuate violently from year to year, production took a decided jump after 1940. Shortage of sugar incident to World War II was of course a contributing factor during the years 1940 to 1945, but improved quality then available allowed popcorn to maintain its competitive advantage after 1945. Averages for the last three decades

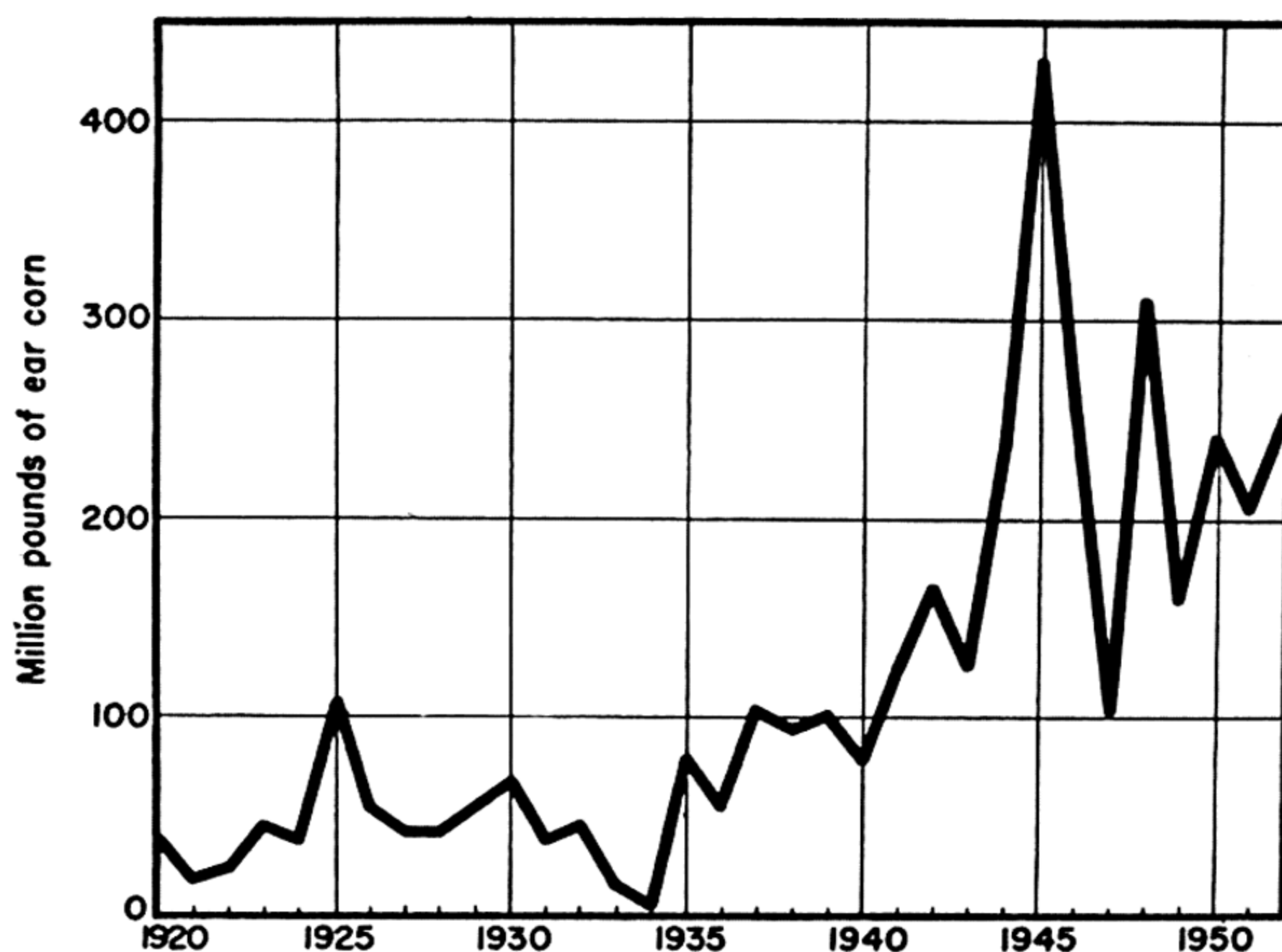


FIG. 2. Annual production of popcorn in 12 principal producing states. From data of Crop Reporting Board, Bureau of Agricultural Economics, U. S. Department of Agriculture.

from estimates issued by the Agricultural Marketing Service of the United States Department of Agriculture are as follows:

1921-30	48,626,300 lb. annually
1931-40	61,307,800 lb. annually
1941-50	214,428,600 lb. annually

Breeding of popcorn hybrids is much the same as for dent hybrids. Yield, standing ability, time of maturity, resistance to diseases and insects, etc., must all be considered. In addition, paramount emphasis must be given to popping expansion and quality. Frequently an experimental hybrid that is outstanding in yield and other agronomic qualities must be discarded because of mediocre popping expansion. The trade has become thoroughly quality conscious and realizes that its product must have excellent popping expansion and quality to meet market competition.

The development of successful hybrids in popcorn and their introduction to the public has been entirely the work of a few state agricultural experiment stations and the United States Department of Agriculture. The early work on hybrids has already been reviewed in some detail (Brunson, 1937). Hybrids that have been approved and released

for commercial production by the agricultural experiment stations are as follows:

Minnesota Agricultural Experiment Station

MINHYBRID 250 (White)

MINHYBRID 251

MINHYBRID 252

Kansas Agricultural Experiment Station in co-operation with U.S.D.A.

K4 (same as P32)

Purdue Agricultural Experiment Station in co-operation with U.S.D.A.

P20 P31 P38

P22 P32 (same as K4) P202

Iowa Agricultural Experiment Station

IOPOP 5 (White)

IOPOP 6

IOPOP 7 (White)

A number of hybrids produced by commercial companies are now also on the market. Reports of extensive performance tests by the Purdue Agricultural Experiment Station and the Iowa Agricultural Experiment Station of hybrids in commercial production and promising experimentals are given annually in the "Popcorn Merchandiser," a monthly trade journal published by the International Popcorn Association, 110 N. Franklin St., Chicago 6, Illinois.

The release of inbred lines Sg16, Sg18, 30A, Sg32, and SA24, all of the lines in the then approved hybrids of the Kansas and Purdue Agricultural Experiment Stations, was announced December 1, 1945. The policy now in effect at the Purdue Station is that germ-plasm lots (100 kernels) of parent inbreds will be released to interested seedsmen and processors the same year that seed of a new approved hybrid is available for production. The Minnesota Station has also released all inbred lines in its approved popcorn hybrids, but thus far the Iowa Station has not released any of its inbred lines of popcorn.

VI. Cross Sterility

One of the serious problems of the popcorn producer has been with dent corn contamination in his crop. Occasional grains of corn pollen can be carried as far as 2 miles by the wind under favorable conditions, and it is impossible to find perfect isolations for seed fields in a good corn-growing area. In addition, many popcorn hybrids require different dates of planting for the pollen parent and seed parent in order that they may flower together, and it is very difficult to obtain perfect timing every year. As a result, there is always some contamination by dent corn in present-day popcorn hybrids, ranging from well under 1 per cent to as high as 20 per cent in exceptional cases. The outcrossed

ears, intermediate between popcorn and dent corn and frequently referred to as "horse corn," are no good for popping and are too hard to feed without grinding. This contamination represents a serious loss to the producer both in lowering the yield of merchantable product and in cost of sorting.

It has been known for a long time that certain varieties of popcorn could not be fertilized by certain other varieties of popcorn or by sweet corn or dent corn. This is the reason that a few rows of STRAWBERRY popcorn in the garden will breed true year after year. It also explains why some of the open-pollinated varieties such as JAP HULLESS and SOUTH AMERICAN were relatively free from contamination, whereas seed of other varieties such as QUEEN GOLDEN and SUPERGOLD frequently showed mixture with field corn. It has recently been found (Nelson, 1952) that this behavior is due to an allelic series Ga^s , Ga , ga located on the fourth chromosome. Nelson has tested many varieties for cross-sterility and lists them in the following categories:

<i>Cross-sterile</i>	<i>Neutral</i>	<i>Normal</i>
SOUTH AMERICAN	WHITE RICE	SUPERGOLD
JAP HULLESS		BABY GOLDEN — 1
BLACK BEAUTY (Rice type)		EARLY YELLOW
RED		All dent corns
OHIO YELLOW		All sweet corns
AMBER PEARL		
YARLING YELLOW		
STRAWBERRY		
BABY GOLDEN — 2		
TOM THUMB		

Any "normal" variety is readily fertilized by pollen from any other corn including dent and sweet varieties. Any "cross-sterile" variety can be fertilized only by pollen of itself, by another "cross-sterile" or "neutral" variety, or by a hybrid involving a "cross-sterile" or "neutral." A "neutral" variety is perfectly fertile with any other corn either as a pollen parent or as a seed parent.

It is relatively easy to transfer this gene for cross-sterility from one inbred to another in a backcrossing program with appropriate tests. Such work is already well under way (Nelson, 1953b), particularly with the widely used "normal" SUPERGOLD inbreds and gives promise that in the not too distant future their cross-sterile counterparts will be available with which to produce hybrid seed uncontaminated with dent corn.

VII. Pop-Dent Recoveries

Most popcorn hybrids do not have as good standing ability as the best dent hybrids. This is no doubt due to a combination of factors in-

cluding the relatively small amount of breeding work done to date on popcorn compared to dent corn, the restrictions placed on selection for agronomic characters where popping expansion is of the utmost importance, and the relatively poor standing ability of some of the original open-pollinated popcorn varieties. The Iowa Agricultural Experiment Station has studied the possibility of transferring the standing ability of some of the proved dent lines with strongest stalks and best root systems to popcorn by the backcross method.

The first question to be answered was how much dilution with dent corn could the popcorn tolerate and still retain good popping expansion. Crumbaker *et al.* (1949) studied the popping expansion and kernel starchiness of crosses between popcorn and dent inbreds together with first and second backcross generations in comparison with the parental inbreds. They concluded that inbred lines of popcorn varied in their ability to transmit popping volume to their progeny, but that in general it was necessary to backcross twice to recover the popping expansion of the original parent.

In a later report on the same project, Johnson and Eldredge (1953) state that although the popping expansion of recovered lines after one and two generations of backcrossing was lower on the average than the popcorn parent, occasional selections from these backcrosses were equal or superior to the popcorn parent. Recovered lines showed some improvement over their parents in root lodging when tested in three-way crosses. No data are presented to evaluate stalk breaking resistance of the recoveries in crosses. The further progress of this breeding method and utilization of recovered lines in successful hybrids will be watched with interest.

VIII. Production and Utilization

Only 11 or 12 states are important commercial producers of popcorn and these are reported in the annual crop estimates. Previous to 1940 the total commercial acreage was less than 0.1 per cent of the corn acreage of the country, but since 1940 it has averaged about 0.2 per cent, although it fluctuates considerably from year to year. Each December the Crop Reporting Board, Agricultural Marketing Service, United States Department of Agriculture issues estimates of the popcorn acreage, yield per acre, production, and price by states for the current year, together with revised estimates of the same items for the previous year. On the basis of these revised estimates, Iowa always ranked first in production from the time these estimates started in 1912 up to and including 1946. For the period 1947 through 1951 Illinois was the chief state in popcorn production, with Iowa or Indiana second. Revised

TABLE I

ACREAGE, YIELD, PRODUCTION, AND PRICE OF COMMERCIAL POPCORN IN PRINCIPAL
PRODUCING STATESFrom Crop Reporting Board, Bureau of Agricultural Economics, U. S. Department of
Agriculture

<i>Year</i>	<i>Area harvested, acres</i>	<i>Yield per acre, pounds</i>	<i>Production, pounds</i>	<i>Season average price,^a dollars</i>
1920	22,300	1,633	36,410,000	4.22
1921	10,700	1,729	18,495,000	3.11
1922	14,800	1,550	22,946,000	2.83
1923	24,600	1,799	44,254,000	5.13
1924	30,800	1,205	37,100,000	2.88
1925	66,100	1,589	105,018,000	2.93
1926	42,400	1,265	53,615,000	2.56
1927	25,500	1,651	42,098,000	2.34
1928	31,700	1,334	42,272,000	2.58
1929	40,800	1,315	53,633,000	2.74
1930	56,200	1,189	66,832,000	2.63
1931	34,400	1,084	37,292,000	1.94
1932	34,600	1,234	42,706,000	1.24
1933	13,100	1,178	15,435,000	1.19
1934	13,400	391	5,246,000	4.98
1935	83,600	949	79,312,000	2.29
1936	57,890	976	56,508,000	2.76
1937	86,100	1,205	103,782,000	1.69
1938	61,850	1,526	94,370,000	1.58
1939	64,500	1,555	100,294,000	1.41
1940	56,450	1,384	78,133,000	1.57
1941	96,475	1,299	125,323,000	2.07
1942	100,250	1,637	164,101,000	2.92
1943	89,650	1,410	126,432,000	4.82
1944	174,800	1,343	234,747,000	3.77
1945	311,900	1,372	427,780,000	3.69
1946	154,600	1,637	253,092,000	3.51
1947	82,500	1,240	102,325,000	4.72
1948	159,400	1,939	309,125,000	4.33
1949	98,700	1,614	159,291,000	3.23
1950	143,000	1,693	242,070,000	3.16
1951	135,100	1,518	205,149,000	4.34
1952	170,600	1,572	268,134,000	4.44
1953 ^b	191,700	1,609	308,428,000	3.75

^a Received by farmers per 100 pounds of ear corn.^b Preliminary.

figures for 1952 and preliminary figures for 1953 place Indiana first and Illinois second. Thus there seems to be a definite trend for the center of production to be moving east. In addition to Iowa, Illinois, and Indiana, the states of Ohio, Kentucky, Missouri, and Nebraska are usually important in popcorn production. Following years of low production with little carry-over there is a distinct tendency to increase acreage in Texas and Oklahoma, where the earlier maturing crop can take advantage of the strong demand before the main crop in the northern states is ready for market. Acreage, yield, production, and price by years are given in Table I for popcorn grown in the commercially important states.

Most of the commercial popcorn is grown under contract and delivered on the ear to processors who temper it to the proper moisture content, shell, clean, and sack it for market. It is then distributed by the bag or by the carload to vendors, theater chains, manufacturers, and packagers on its way to the ultimate consumer. High-quality popcorn in moisture-proof small packages for home use is becoming an increasingly important outlet.

REFERENCES

- ANONYMOUS. 1946. New popcorn volume tester. *The Popcorn Merchandiser* 1 (No. 6), 11-13.
- BRUNSON, A. M. 1931. Popcorn selection for added popping expansion would pay large growers. *Yearbook Agr., U. S. Dept. Agr.* 1931: 441-443.
- BRUNSON, A. M. 1937. Popcorn breeding. *Yearbook Agr., U. S. Dept. Agr.* 1937: 395-404.
- BRUNSON, A. M., and SMITH, G. M. 1945. Hybrid popcorn. *J. Am. Soc. Agron.* 37: 176-183.
- BRUNSON, A. M., and SMITH, G. M. 1948. Popcorn. *U. S. Dept. Agr. Farmers' Bull.* 1679 (Rev.).
- CARR, R. H., and RIPLEY, E. F. 1920. What puts "pop" in popcorn? *Proc. Indiana Acad. Sci.* 1920: 261-270.
- CRUMBAKER, D. E., JOHNSON, I. J., and ELDREDGE, J. C. 1949. Inheritance of popping volume and associated characters in crosses between popcorn and dent corn. *Agron. J.* 41: 207-212.
- DEXTER, S. T. 1946. Conditioning popcorn to the proper moisture content for best popping. *Michigan Agr. Expt. Sta. Quart. Bull.* 29: 64-69.
- DUNCAN, J. R. 1936. Culture and use of popcorn. *Michigan Agr. Expt. Sta. Circ. Bull.* 148.
- ELDREDGE, J. C., and LYERLY, P. J. 1943. Popcorn in Iowa. *Iowa Agr. Expt. Sta. Bull.* P54.
- ELDREDGE, J. C., JOHNSON, I. J., and RICHARDSON, C. H. 1953. Cold storage of popcorn. *The Popcorn Merchandiser* 7 (No. 12), 32-46.
- ERWIN, A. T. 1949. The origin and history of popcorn. *Agron. J.* 41: 53-56.
- JOHNSON, I. J., and ELDREDGE, J. C. 1953. Performance of recovered popcorn inbred lines derived from outcrosses to dent corn. *Agron. J.* 45: 105-110.

- LYERLY, P. J. 1942. Some genetic and morphologic characters affecting the popping expansion of popcorn. *J. Am. Soc. Agron.* **34**: 986-999.
- MANGELSDORF, P. C., and SMITH, C. E., JR. 1949a. A discovery of remains of primitive maize in New Mexico. *J. Heredity* **40**: 39-43.
- MANGELSDORF, P. C., and SMITH, C. E., JR. 1949b. New archaeological evidence on evolution in maize. *Botan. Museum Leaflets, Harvard Univ.* **13**: 213-247.
- NELSON, O. E., JR. 1952. Non-reciprocal cross-sterility in maize. *Genetics* **37**: 101-124.
- NELSON, O. E., JR. 1953a. Hybrid popcorn performance tests—1952. *Purdue Agr. Expt. Sta. Mimeo* **BP-56**.
- NELSON, O. E., JR. 1953b. A genic substitute for isolation in hybrid corn seed production. *Econ. Botany* **7**: 382-384.
- PETERSON, E. L., ELDREDGE, J. C., and JOHNSON, I. J. 1949. Predicting the performance of popcorn hybrids from single cross data. *Agron. J.* **41**: 104-106.
- SMITH, G. M., and BRUNSON, A. M. 1947. Hybrid popcorn in Indiana. *Purdue Agr. Expt. Sta. Bull.* **510**.
- STEWART, F. C. 1923. The relation of moisture content and certain other factors to the popping of popcorn. *New York State Agr. Expt. Sta. Bull.* **505**.
- STEWART, F. C. 1936. The relation of age and viability to the popping of popcorn. *New York State Agr. Expt. Sta. Bull.* **672**.
- WEATHERWAX, P. 1922. The popping of corn. *Proc. Indiana Acad. Sci.* **1921**: 149-153.
- WILLIER, J. G., and BRUNSON, A. M. 1927. Factors affecting the popping quality of popcorn. *J. Agr. Research* **35**: 615-624.

CHAPTER XI

Sweet Corn

GLENN M. SMITH

I. Introduction

One recessive gene, *su*, is responsible for the difference in composition of a sweet-corn kernel and that of dent corn. This gene prevents the conversion of part of the sugar into starch.

Kempton (1926) states that genetic evidence indicates that sweet corn is a mutant from field corn. E. W. Lindstrom in 1929 found a single sweet-corn kernel as a mutant in a series of pedigree cultures of dent corn. Four generations were tested and crossed with normal sweet corn, and all proved the original kernel to have been a true mutant from field corn. Some varieties, such as GOLDEN BANTAM, were derived from flint corn and the others, constituting the major portion, from the dent corns.

Although most of the sweet-corn acreage is confined to the northern half of the United States and southern Canada, it is rapidly becoming an important crop in Florida. High temperatures tend to convert the sugar in the kernel into starch, and for this reason sweet corn has not been too successful as a spring or summer crop in the South. Another consideration has been the occurrence of the corn-ear worm, which is much more prevalent in the southern states owing to the milder winters. Bacterial wilt has also been a limiting factor, although the development of resistant hybrids has tended to reduce damage from this disease.

At the present time much work is being done by the Regional Laboratory at Charleston, South Carolina, toward the development of adapted hybrids which can be grown in the South and which have quality, yield, and insect and disease resistance. The various experiment stations are co-operating in conducting trials of northern-grown hybrids to determine their adaptation to the various sections of the South.

II. History

According to historical accounts, the origin of sweet corn dates back to 1779, when a member of the Sullivan expedition against the Six

Nations brought back a few ears of sweet corn, which was called papoon corn (Erwin, 1934). Sweet corn was first offered to the public in 1828 by Thorburn. Since that time the number of types and varieties has increased until at the time of the first efforts at inbreeding and crossing there were approximately 180 open-pollinated white and 50 yellow varieties, of which many had a number of synonyms.

According to Singleton (1944) Noyes Darling, a lawyer living in New Haven, Connecticut, was probably the first sweet corn breeder to produce a hybrid before the rediscovery of Mendel's laws. In 1836 he crossed a very early yellow corn with a white sweet type by detasseling the yellow variety. From this hybrid seed he selected an early white sweet corn which produced large ears and straight rows and which was more productive than either parent.

Halstead and others in New Jersey in 1898 combined the best features of BLACK MEXICAN and EGYPTIAN, a white-kerneled variety. They observed xenia in the crossed kernels and selected the black seeds from the white ears. In 1900 they began artificial inbreeding in open-pollinated lines in an effort to improve stocks for earliness and higher percentages of two- and three-eared stalks.

In 1907, Pearl and Surface in Maine undertook the production of seed adapted to that state. They started an inbreeding program and after discarding the poorer lines made experimental crosses, thus using the performance of the progeny as a basis for the selection of breeding stock.

Huelsen and Gillis began a breeding program in Illinois in 1926 with special emphasis on tenderness. They observed tender pericarp in some dent corns as well as in sweet corn.

The first hybrid sweet corn to be grown extensively was a white type known as REDGREEN, developed at the Connecticut Agricultural Experiment Station by D. F. Jones and released for commercial production in 1924. It was especially adapted to New England, central New York, and certain sections of the northern states.

The breeding program at the Purdue University Agricultural Experiment Station was instituted in 1920 in co-operation with the United States Department of Agriculture. The first hybrid released under this project was GOLDEN CROSS BANTAM, which was made available for seed production in 1933 (Smith, 1933). For two years prior to that time PURDUE 39 (the seed parent of GOLDEN CROSS BANTAM) was used for top crossing with various open-pollinated yellow varieties to produce high-yielding canning types. When stocks of GOLDEN CROSS BANTAM became readily available, the production and use of top-crossed seed practically ceased. Wilt epidemics in 1932 and 1933 destroyed entire fields of sus-

ceptible varieties such as GOLDEN BANTAM and EARLY CROSBY in the Midwest and demonstrated the relative resistance of GOLDEN CROSS BANTAM when grown under these conditions. Quality and yield were satisfactory, and it eventually became the standard for judging other hybrids which were introduced by seedsmen and experiment stations. The popularity of this hybrid increased the demand for others, particularly for earlier types which would be resistant to wilt. PURDUE 39 carries factors for yield, vigor, and wilt resistance, and it is estimated that this inbred or its derivatives constitute one parent for nearly 80 per cent of all hybrid sweet corn seed produced.

Sweet corn breeders at various experiment stations are producing and releasing hybrids in increasing numbers and it is now possible for a grower to select a variety suited to his needs. Illinois, Iowa, Wisconsin, Connecticut, New Jersey, Maine, Massachusetts, and Pennsylvania have extensive sweet corn breeding projects, and several have released excellent hybrids to the trade. A few seed companies and canning organizations have their own programs and are marketing many meritorious varieties.

III. Uses of Sweet Corn

1. Canning

Most of the acreage planted to sweet corn is used for canning purposes. In 1952 the total area planted for processing was 487,500 acres, with an average yield of 3.13 tons per acre. Before the introduction of hybrid sweet corn, canners were inclined to buy seed at the lowest possible price consistent with satisfactory germination. Through a program of education the importance of buying artificially dried seed was emphasized and thus became an important consideration to the buyer. After the introduction and acceptance of GOLDEN CROSS BANTAM as a canning corn, cannery managements have become seed quality conscious and are now demanding good seed, graded and treated with a disinfectant to insure good germination.

There are two methods of canning now in use:

a. Whole-Kernel. In this type of processing the ears are first blanched to set the endosperm, and the kernels then are removed from the cob by a series of knives set to cut at a uniform distance just above the glumes. The cut corn is then packed in a brine or canned under vacuum with a very small amount of brine.

Only the younger corn, having a moisture content of 72 to 75 per cent, is used for this purpose. Hence it is evident that the corn must have a tender pericarp and good flavor, for in most cases no flavor corrective can be added. Whole-kernel canning in 1930 was an expensive

operation requiring continuous sorting of ears from open-pollinated varieties to obtain the most tender corn. With the introduction of hybrids, the uniformity of maturity made it possible to harvest an entire field at a given moisture content and thus reduce sorting costs.

b. Cream-Style. Corn for this type of processing ranges in moisture from 68 to 72 per cent. The kernels are cut from the cob and the cob is then scraped by revolving wheels which remove the residue from the uncut bases of the kernels. In this process a brine of salt and sugar is added and corn starch may be included to insure proper consistency of the mixture. From this it is evident that the flavor of the variety used is not a serious consideration because poor flavor can sometimes be altered by the use of a special brine. A "homogenized" type of processing is relatively new and is restricted to relatively few canneries. It is in a sense a combination of the cream-style and whole-kernel methods. The kernels from the cream style cutters are macerated and thoroughly mixed with the juices and the whole kernels are added.

2. Freezing

Commercial and home freezing of sweet corn emphasizes the importance of quality in the raw product. Tenderness and flavor are the two factors which contribute most to the production of high-grade frozen corn.

3. Market Corn

Most recent figures (Anonymous, 1953a) indicate that 360,000 acres are planted to sweet corn for market and home garden purposes. Florida, where sweet corn production for the northern markets has become a big business, accounts for over 35,000 acres. There are three reasons for the remarkable growth in this industry:

1. The breeding of new hybrids suitable for culture in the South—both for local use and for shipment northward.

2. The availability of new insecticides and fungicides for the control of harmful insects and diseases, especially the ear worm and the leaf blights.

3. The development of improved packing and shipping materials, equipment, and methods (Boswell, 1952).

The most important limiting factor in the production of sweet corn in the South is the northern corn leaf blight caused by *Helminthosporium turcicum*. Up to the present time no resistant hybrids have been developed, and it is necessary to spray to control this disease.

In selecting hybrids for large-scale production the emphasis is placed on hybrids which are prolific, produce attractive ears of good

quality, and are adapted to the climate in which they are to be grown. Resistance to ear-worm damage and bacterial wilt is also of considerable importance.

4. Home Gardens

It is difficult to estimate the total acreage devoted to home gardens. The introduction of home freezers has increased interest in gardens as a source of vegetables for winter use. Many gardeners want early types which will reach the table in late June or early July. Resistance to bacterial wilt is the most serious problem in such varieties, and some of our best early sorts cannot be grown in areas where this disease is prevalent. In the midseason varieties, which are usually frozen, quality is of prime importance and many hybrids are especially adapted to this purpose. Here again prolific varieties are greatly in demand.

5. Drying

The use of quick-freeze equipment has practically eliminated the drying of sweet corn, although there are a few localities where this method of processing is popular.

IV. Culture

1. Soil

In most respects sweet corn does not differ greatly from dent corn in its soil requirements. In general a well-drained moderately heavy soil gives best results for the canning factory. Adequate moisture during the latter part of the growing season assures a good yield of quality corn. For the market a light soil will insure an earlier crop to command top prices.

2. Fertilizers

Commercial fertilizers will produce profitable returns in yields of sweet corn on most soils if carefully selected and properly applied. The requirements will vary from state to state, for different soil types, and according to the purpose for which the crop is intended, i.e., whether for processing or for market.

For most of the areas where sweet corn is grown, recommendations by Boswell (1952) include 5-8-5, 5-10-5, or other mixtures having similar proportions of the three elements. Rates of application vary widely with the largest amounts to be used on the sandy soils of the Southeast. In the better soils of the Corn Belt, recommendations vary from 400 to 700 pounds per acre, preferably applied in bands at time of planting.

A plentiful supply of plant nutrients should be available early in the life of the sweet corn plants, especially when they are being produced for the market, and there should be enough to maintain steady, rapid growth until harvest.

Investigations at the Illinois Station (Huelsen, 1936) indicated that nitrogen-carrying fertilizers could not be added profitably to a phosphate-potash fertilizer. Most growers use 75 to 125 pounds 0-16-6 per acre applied around the hill. In Illinois nitrogen salts have given variable results, and under certain conditions the yields may be seriously impaired by nitrogen applications. It is therefore advisable for the grower to use them sparingly unless experimental results have definitely shown their value.

At Wisconsin (Anonymous, 1939) increases ranged from 38 to 52 per cent through the use of a complete fertilizer. Side dressing showed promise depending on soil type, its fertility, fertilizer used, and soil moisture.

On light soils in New York (Thompson *et al.*, 1941) nitrogen had greater effect on yield than phosphorus or potash. With early corn the equivalent of 2.5-10-10 produced three times the weight of marketable ears than the same amount of 0-10-10. Increasing N to 5 per cent increased the yield nearly 50 per cent over 2.5 N. Side dressing with 25 pounds of N in addition to 5 per cent resulted in still greater increase. With late corn the increase was less than with early types. Phosphorus had greater effect on yield than potash.

3. Spacing

Investigations on the spacing of sweet corn have been conducted at several experiment stations, and in all cases it was apparent that closer spacing results in more ears per acre, but the ear size decreases. Growing sweet corn in drilled rows is usually limited to the early market garden types raised by truck growers. Corn for processing is predominantly planted in checked hills.

At the Illinois Station, Huelsen (1942) conducted extensive trials with the COUNTRY GENTLEMAN and NARROW GRAIN EVERGREEN varieties which indicated that a tall-growing vigorous variety like NARROW GRAIN EVERGREEN is most productive when planted in heavier stands than COUNTRY GENTLEMAN. In Central Illinois, COUNTRY GENTLEMAN seed should not be planted closer than 40 × 40 inches with three plants per hill. NARROW GRAIN EVERGREEN may be planted 38 × 38 inches with three plants per hill. It is well to avoid excessive planting rates because losses in yield may be heavy in a dry year. For drill planting it is

recommended that the distance be 8 inches for EVERGREEN and 14 inches for COUNTRY GENTLEMAN, with rows 40 inches apart.

Trials at the Maine Station (Anonymous, 1939) indicated an increase in ear size and length when the distance between plants was increased. The maximum effect was attained at a 12-inch distance for small varieties and at 14 inches for larger types. Data indicate that the optimum distance is influenced considerably by soil moisture and fertility.

Recommendations for drill planting according to Beattie (1936) are as follows:

For medium-sized varieties: 12 to 14 inches in 32-inch rows or 12 inches in 36-inch rows.

For large varieties: 14 inches in 36-inch rows or 12 inches in 40-inch rows.

For planting in check rows three or four plants per hill are best, with the hills 32×32 inches for small types, 36×36 for medium, and 40×40 for large varieties.

4. *Planting*

Processors are becoming increasingly conscious of the importance of a uniform maximum stand of sweet corn which will mature evenly. For this reason they are demanding graded seed and are using proper planting plates to handle the indicated grade. The larger varieties of sweet corn yield best at 14,500 plants per acre, according to trials at Geneva, New York (Anonymous, 1953b). A survey showed that most fields in that state had less than this plant population, owing primarily to careless adjustment and operation of planting equipment. Other causes of poor stand were improper planting plates, ungraded seed, poor seedbed preparation, insects, damping-off, birds, and weeds. Sweet corn seed varies from 1500 seeds or less per pound to as high as 4000 per pound. This fact must be considered in estimating pounds of seed to use per acre.

5. *Tillering*

Most varieties of sweet corn tiller to some extent, especially the earlier sorts. The value of the tillers has often been questioned by growers, and many practice removal in the belief that they are detrimental to the plant. Dungan (1931) and Jones *et al.* (1935) have shown that tillers are not detrimental but are distinctly useful in maturing sweet corn, especially market types, where early production of large ears is of prime importance.

Thompson *et al.* (1930) conducted experiments to determine the effects of removing suckers. They found that late removal of suckers markedly decreased yield; this indicated that removal after the suckers reach considerable size is injurious since it reduces the manufacturing area of the plant at a time when it is difficult for the main stalk to replace the loss.

6. Harvesting

a. Time of Harvest. Fields for canning are harvested when the corn is in the proper condition for the desired type of pack, i.e., for whole-kernel or cream-style, as previously described.

The date of harvesting will vary with the locality where grown and the variety, and time of planting may vary from season to season in the same area. The kernels should have reached full size and be plump and full of milk. At this stage the silks outside the husks have turned dark brown and dried. High quality is closely associated with the sugar content of the kernels. In the ripening process the sugar changes rapidly to starch, the kernels passing through the pre-milk, soft-dough, and hard-dough stages. If the corn is harvested too early, the yield in tons per acre and in cases per ton will be low and the product will lack consistency. If the corn is too mature, the canned product will lack flavor, be starchy, and have tough pericarps.

According to Huelsen and Michaels (1937) there are three distinct climaxes in maturity:

1. Period of maximum yield and percentage of prime husked ears—moisture content 70 per cent.
2. Period of maximum yield of sorted unhusked ears—moisture content 66.4 to 68.3 per cent.
3. Period of maximum yield of sorted husked ears—moisture content 63.0 to 65.2 per cent.

For cream-style canning the moisture content of the raw corn is 70 per cent, and for whole-kernel the content should be above 70 per cent. Experienced "field men" determine the day on which a field is ready for picking, and the corn is harvested and hauled to the factory at that time. For many years canners depended upon the "thumbnail test" to determine the maturity of sweet corn for the factory. This involved pressure upon the kernel with the thumbnail in such a way as to force out the juice, and the consistency of this juice indicated the relative maturity. In recent years canners have adopted moisture testers or the succulometer described by Kramer and Smith (1946) to measure the maturity of raw and canned corn. It enables the operator to determine the maturity of raw corn at any stage during the canning operation

and also has been accepted as an indication of the tenderness of the kernels.

The period from silking to maturity will vary with the variety and the season, but may be used as an indication as to the approximate date of canning condition. In general this period is somewhat shorter in the case of hybrids than in the open-pollinated varieties. In the Midwest the early hybrids in a normal season are usually in edible condition in 14 to 16 days after silking, the midseason types in 16 to 18 days, and the later types such as COUNTRY GENTLEMAN and EVERGREEN in 18 to 21 days. In other areas this period may be somewhat longer.

Huelsen and Michaels (1937) found that the silks emerge according to a skew curve. The lower ear shoots lagged from one to two days behind the upper shoots. This lag tends to widen the range of maturity in sweet corn and emphasizes the desirability of selecting plants with single ears or those types which produce ears silking at the same time.

Corn for freezing should be picked at about the same state of maturity as for whole-kernel canning, namely at 70 to 72 per cent moisture. For a high-quality product a special effort is made to process the corn as quickly as possible after harvesting in order to maintain a high level of sugar content, together with tenderness of pericarp.

The same general principles as to time of harvesting for processing apply equally to corn for market, except that in some cases the demand is for younger corn, i.e., with approximately the same moisture content as for freezing. This corn is sold on the basis of number of ears, usually expressed in dozens, and the grower does not take any loss owing to the lighter weight of younger ears as would be the case if he were selling to a processor.

b. Methods of Harvesting. In areas where labor is a problem, growers of corn for processing have been greatly benefited by the development of mechanical pickers especially adapted for sweet corn. This method of harvesting also has the advantage of night use in rush periods, for the machines can be equipped with lights and operate 24 hours a day. The newer models pick a higher percentage of good ears than hand-pickers. Some machines under good conditions may pick as much corn per hour as 15 or 20 men. However, although many processors use machines, the majority of the acreage is still hand-harvested.

Practically all corn for market is picked by hand, loaded into trucks, and hauled to the packing shed. In the Belle Glade district in Florida, "mobile packing sheds" are used very effectively. Hand-pickers throw the ears on conveyors which transport them to workers who pack the ears in crates. The crated corn moves on conveyors to trucks which haul the corn to cooling sheds.

V. Problems in Sweet Corn Breeding

Quality, productivity, and resistance to insects and diseases are the prime considerations in a sweet corn breeding program. Most of the requirements for a good sweet corn hybrid or variety are the same for the market and for processing. The market gardener, however, demands a variety which produces a maximum number of attractive ears of good quality combined with resistance to insects and diseases. Earliness is also an important characteristic for this form of marketing.

The processor is especially concerned with quality, cutting percentage, and yield, in that order. Tillering habit, uniformity of maturity, and color of silk inside the husk are also of particular interest to processors and must be given serious consideration in the search for better hybrids. Earliness does not influence the canner or freezer in the selection of a hybrid as it does the market gardener.

1. Quality

The quality of sweet corn, whether canned or frozen, determines its market value. This is also true to some extent of fresh corn. Among the factors considered in estimating the quality in whole-kernel canned corn are color, absence of foreign matter, cut, maturity, and flavor. Of the total points involved, the Bureau of Agricultural Economics has scored 25 per cent for flavor and 35 per cent for maturity. In view of the stress placed upon the importance of maturity, any attempt to place the grading for quality on a quantitative basis must base the evaluation of the product on the measurement of maturity.

a. Tenderness or Succulence. The value of tenderness depends almost entirely upon the nature of the pressure tester (Culpepper and Magoon, 1924) or tenderometer. The pressure tester consists of a plunger operating in a metal tube with an indicator which registers the amount of pressure at the time the needle punctures the pericarp. The machine may be mounted or may be carried to the field for determinations on ears on the stalk.

The tenderometer is a variation of the pressure tester. The cut corn is placed in a cup with a perforated cover. A plunger with needles to match the perforations is then used to determine the amount of pressure required to puncture the pericarps of the kernels.

At prime canning stage (70 to 72 per cent moisture) practically all varieties studied by Gaessler *et al.* (1940) are tougher than desired. The study indicated that at canning stage hybrids and inbreds differ in the quantity of pericarp and that strains classed as "very tough" when chewed contain 50 to 100 per cent more pericarp than those

classed as "tender." Kernels of tender strains contain 4 to 5 per cent pericarp, medium tender from 5 to 6 per cent, tough from 6 to 7 per cent, and very tough over 7 per cent on a dry-weight basis.

Bailey and Bailey (1938) found that the pericarp decreases in thickness as the kernel matures but that its resistance to mechanical puncture markedly increases. Varietal differences in tenderness and pericarp thickness were evident. Those varieties having the lowest puncture index at a given stage of maturity were generally those with the thinnest pericarp.

Burton (1922) emphasized the fact that general toughness cannot be masked, and it is this fact more than any other which unfavorably affects the quality of canned corn. He found that commercial grades of canned COUNTRY GENTLEMAN corn, as far as they are influenced by maturity, differ only in the proportion of tough and tender kernels present. In further studies of maturity he found that crude fiber analysis showed nothing of value in this respect. He also found that the specific gravity of the kernels had a direct bearing in differentiating old from young and tough from tender corn.

In an attempt to accurately measure toughness Jenkins (1935) undertook chemical studies on raw and canned corn. His investigations revealed that there is a loss of moisture and a definite accumulation of starches and related solids as the kernel matures. It was found that when hot 80 per cent alcohol was used as a solvent, all sugars and some other compounds were dissolved but that starches, hemicelluloses, fiber, and proteins remained insoluble. The proportion of these latter compounds increases in maturing corn; therefore this proportion can serve as an index of the maturity of the raw corn and also as an evaluation of quality in the canned product. However the percentage of alcohol-insoluble residue expressed on a fresh-weight basis cannot be used as an index of the quality of cream-style canned corn because the commercial practice in canning corn by this process is to add more water and live steam to the more mature corn while cooking. This additional water is taken up by the increased amount of starch in the more mature corn.

Haddad (1931) studied the morphological development of the pericarp in a NARROW GRAIN EVERGREEN hybrid and the two inbred parents. The thickness of the ovary wall of the hybrid increased until the tenth day after silking and then decreased in thickness. The ovary wall of the two parents increased in thickness until the fifteenth day and then decreased. The thickness of the ovary wall of the hybrid was less than in either parent at all the corresponding stages between the stage of maximum thickness and maturity.

Doxtator (1937) conducted pericarp studies on a number of GOLDEN

BANTAM hybrids and their parent lines. Inbred lines which gave low pressure test indices tended to produce crosses having a low index. The puncture test index in a date of harvest experiment was positively correlated with date of silking and negatively correlated with yield in 66 hybrids in two test years. Percentage of husk did not appear to be correlated with tenderness. Stage of maturity as measured by percentage of moisture at harvest time was negatively and very significantly correlated with puncture index in the case of four cultures tested.

Johnson and Hayes (1938) crossed a very tender open-pollinated variety and a tough EARLY CROSBY inbred line. The parents showed a consistent difference of approximately 100 units as measured by a puncture tester, and the F_1 between the two was intermediate in puncture tests and also in coefficient of variability.

In a study of the F_3 progeny rows and in first-year selfed lines from backcrosses to the tender parent, lines were obtained with as low a coefficient of variation as the tough inbred parent. The recovery of relatively pure lines having an average puncture test value in the classes intermediate between the parents suggests that several factor pairs condition pericarp tenderness. In backcrosses to the tender pericarp parent selection for tenderness was apparently effective in almost complete recovery of the genotype of the tender parent in the second backcross generation.

In a study to determine the daily change in puncture test values during the period from 18 to 22 days after pollination, a daily increase of approximately 30 units was obtained in one class and 20 units in a later maturing hybrid. Puncture test values from ears pollinated when the silks had been emerged for 1, 3, and 5 days showed an increase of over 20 units for each intervals of 2 days after emergence of silks. These results indicate that the pericarp continues to develop without fertilization for at least 5 days.

Lee and Sayre (1939) used the alcohol-insoluble and total solids methods to study the index of maturity for sweet corn to determine which of 15 hybrids stayed in "fancy" stage over the longest period. Results indicated considerable variation among hybrids as to the length of time the corn remains in edible condition.

Metzger (1933) studied some of the factors affecting quality in canned corn, with special emphasis on the relationship of fertilizers to yield and quality. He used the puncture test to determine the tenderness of corn which had received different fertilizer treatments. He was unable to determine any difference in tenderness due to fertilization, although many hundreds of measurements were made.

Kramer *et al.* (1949) compared various methods of evaluating

quality by mechanical and chemical methods. They found that succulometer readings and moisture tests may be used interchangeably and are very satisfactory in estimating the quality of raw corn as it appears to the consumer before cooking. After cooking these tests are good indicators of succulence and skin characters but not of flavor. The puncture test is inferior to the above as an indicator of raw appearance or succulence but equal or perhaps slightly better for predicting pericarp character and flavor. The factor of length of time in storage had relatively less effect on moisture and succulometer values than on pericarp or taste evaluation. For pericarp and flavor the effect of prolonging the duration of storage was nearly as severe as delaying the date of harvest. The effect of increasing the temperature of storage was not as severe as increasing duration of storage on reduction of quality. Varietal differences were found primarily among the white varieties, where COUNTRY GENTLEMAN samples ranking equally with other varieties in tenderness and flavor tests appeared inferior according to objective tests.

b. Flavor. Flavor is difficult not only to define but also to measure in an objective manner. It is primarily dependent upon the presence of sugars together with intangible flavors which may be due to esters which appear to vary with the variety and inbreds within a variety.

The measurement of the refractive index may be considered a test of flavor, since it measures the soluble solids content which consists largely of sugars (Scott *et al.*, 1945).

Culpepper and Magoon (1924) found that the percentage of sugar in the kernels of green corn changed constantly during the development and ripening of the ear. The total sugar increased rapidly from the time of silking and then decreased rapidly throughout the maturing period. Reducing sugars were high at first and then steadily decreased until maturity. Sucrose increased rapidly to the 15-day stage and then decreased slowly as the corn matured.

These changes in the percentage of sugars profoundly affect the sweetness of the canned product, though the percentage of total sugar is not an exact measure of the sweetness. The percentage of total sugar in the corn canned at the 15-day stage is much higher than at the 20-day stage, but the difference in the sweetness of the two products is not as great as the percentage of sugar would indicate.

Jenkins and Sayre (1936) made a study of the chemical composition of several types of sweet corn and the relation of the constituents to the length of time in days that the corn remained in prime condition. Their results indicated that the hybrid strains studied were superior to the open-pollinated varieties from the standpoint of improved quality,

slower in maturing ears and that they had nearly double the length of "harvest spread," owing to a slower increase in total solids and alcohol-insoluble solids. In the whole-kernel type of canned corn the scores for maturity and for tenderness were directly proportional to the scores for flavor. The percentages of total solids and of alcohol-insoluble solids were lower in the canned than in the fresh corn. The differences in the percentage of sugars during the period studied were not significant between the different types of sweet corn at any stage of maturity. Likewise the percentages of starch did not vary widely between each comparative series of tests.

Straughn (1907) found no correlation between the amount of sugar in corn when in edible condition as compared to the same variety as dried seed. He therefore assumed that in breeding for sugar content it is necessary to make selections when the corn is in the green or canning stage.

In sweet corn the rate at which the percentage of sugar decreases in storage becomes much slower as the supply diminishes, according to Platenius (1939). Under certain conditions there may be an actual increase in the percentage of sugar present. The quantity of sugar present at any one time depends on the rate at which sugar is oxidized in the process of respiration and at the same time is replenished by the conversion of starch to sugar. These two processes may have different temperature coefficients and both are controlled by mass action. Any precooling method is of little use unless cooling below 55°F. can be accomplished. Exposure to 35°F. from a few days to several weeks had no noticeable effect on the subsequent rate of breakdown when the corn was transferred to higher temperatures.

Appleman and Arthur (1919), working with the STOWELL EVER-GREEN variety picked when the water content was 80 per cent, showed that the loss of sugar ceased when the initial total sugar had decreased about 62 per cent and the sucrose about 70 per cent. At 30°C., 50 per cent or most of the total sugar loss occurs during the first 24 hours of storage; at 20°C., 25 per cent loss occurs; and at 10°C. (good refrigerator temperature) only about 15 per cent is depleted during the same period. The rate of sugar loss, until it reaches 50 per cent of the initial total sugar and 60 per cent of the sucrose, is doubled for every increase of 10° up to 30°C. Most of the decrease in the percentage of sugar in green sweet corn during storage is due to condensation to polysaccharides, chiefly starch.

Doty *et al.* (1945) undertook to find out if inbred lines of sweet corn used in the development of new hybrids differed in their chemical constitution and stability for several hours after harvest. Thirty-four

GOLDEN BANTAM, COUNTRY GENTLEMAN, and EVERGREEN inbreds, three yellow hybrids, and three EVERGREEN hybrids were studied over a four-year period. The different inbreds and hybrids differed markedly in their sugar content at harvest time and in the rapidity with which sugars were changed to polysaccharides during storage at 68°F. The condensation of sugars to polysaccharides was more rapid at 68°F. than at 98°F. after the very early part of the storage period.

The rate of sugar loss for each strain was similar from year to year, indicating that the internal factors which affect the change from sugars to polysaccharides during storage are controlled in part by the genetic constitution of the plant. These results emphasize the importance of selecting inbreds for the production of hybrids that will retain their sugar content during the holding period before marketing or processing.

Investigations now in progress at the Iowa Station indicate that there is more oil in the dry kernel than at the canning stage. Oil content increases slowly from the stage of 15 days after pollination until approximately 25 days later and then remains fairly constant. Proteins in the kernel are high 10 days after pollination but decrease very rapidly for the next 30 days, after which they level off. There is 50 to 60 per cent less protein at the canning stage, 20 to 22 days after pollination, than 10 days after pollination.

2. Yield

Corn for the market is sold by the dozen, and consequently the grower is concerned with the number of ears per acre. For processing the producer demands a high tonnage per acre, and the canners and freezers want the maximum amount of corn per ton.

Total yield of green corn is the result of a proper balance of variety, season, and crop management. The yield of cut corn from a given amount of green corn is largely dependent upon variety and maturity.

The variety or hybrid used for processing must be productive enough to satisfy the grower and have a cutting percentage high enough to satisfy the processor (Haber, 1949). Hybrids vary in yield from year to year owing to differences in growing conditions, but there seems to be little variation in cutting percentage in the same hybrid from year to year. Furthermore a reduction or increase in cutting percentage is not entirely associated with higher yields of green corn. Tonnage and cutting percentage are not correlated. Trimming in the factory for insect and disease damage will naturally reduce the cutting percentage.

Straughn (1907) at Maryland determined the relative percentage of husks, cobs, and kernels on open-pollinated STOWELL EVERGREEN. The husks accounted for 31 to 33 per cent of the total weight of the ear, and

the amount of the cut corn ranged from 28 to 38 per cent. Most sweet corn breeders select for deep kernels and small cobs to insure a high percentage of cut corn.

Haber (1949) found a wide variation among hybrids as to the percentage of usable corn on the ears. Some hybrids yielded as low as 28 per cent cut corn and others as high as 40 per cent.

Kramer (1946) showed that total yield does not vary materially over a considerable period of time, but that the yield of cut kernels does increase with increasing maturity. However, whereas maximum yields of GOLDEN CROSS BANTAM and COUNTRY GENTLEMAN are reached when the material may be expected to produce young (extra standard grade) quality, the maximum yields of ARISTOGOLD EVERGREEN and NARROW GRAIN EVERGREEN are not reached until the material averages low standard in quality.

Cutting percentage is dependent upon kernel pattern, especially depth of grain. NARROW GRAIN EVERGREEN and COUNTRY GENTLEMAN have been selected for this characteristic over a long period of time. NARROW GRAIN EVERGREEN has a deep narrow kernel with usually 18 or more rows per ear. The COUNTRY GENTLEMAN variety has a so-called "zigzag" arrangement of kernels due to the development of both ovules (Poole, 1937). Huelsen and Gillis (1929) found that the rowed kernel arrangement in sweet corn is incompletely dominant over the zigzag arrangement as shown in F_1 progenies.

3. *Resistance to Insects and Diseases*

The corn earworm is the most destructive insect to sweet corn in practically all sections of the United States, and every effort is being made to develop resistant hybrids. Poole (1937) has conducted extensive investigations to develop earworm resistant strains, and workers at various stations are working along similar lines.

The European corn borer is second in importance to the earworm and unless controlled by spraying or dusting may cause heavy financial loss. Where the borer enters the ear it may follow the bases of the kernels and thus escape detection on the sorting table. Worm fragments found in canned corn may result in condemnation of part or all of a season's pack.

The corn flea beetle is a serious problem as a vector of the organism causing bacterial wilt (*Phytophthora stewartii* or *Bacterium stewartii*).

Bacterial wilt causes enormous damage in seasons following a mild winter. However, breeders realize the importance of developing resistant hybrids, and many of the present-day varieties exhibit marked resistance (Smith, 1933). Wellhausen (1937) found that resistance to

bacterial wilt is apparently governed by three factors which he designated Sw_1 , Sw_2 , Sw_3 in the order of importance, i.e., an inbred having Sw_2 was more resistant than one having Sw_3 . A line having all three was designated as highly resistant. Investigations by Ivanoff and Riker (1937) indicated that tall and late hybrids were, as a rule, more resistant than short and early hybrids.

Ear smut is of prime consideration in sweet corn production, and there is a wide variation in resistance in sweet corn hybrids. An early commercial hybrid, EARLY GOLDEN, produced 76 per cent smutted top ears in trials at the Purdue Station in 1953, as compared to no damage in hybrids in adjacent rows (Smith, 1953).

Sweet corn is especially susceptible to the northern corn leaf blight and the southern leaf blight described by Ullstrup in Chapter XII. The former diseases causes severe losses in the spring crop in Florida except in those areas where a rigid spray program is practiced. Sweet corn breeders are now searching for resistant lines which will eliminate or reduce the necessity of spraying.

4. *Color of Kernels*

Market demands for color in green corn are not so exacting as for processing. For market corn a good golden color in yellow corn is acceptable without regard to shade. Processors, especially canners, alter their ideas as to color over a period of years. When first introduced GOLDEN CROSS BANTAM was considered too light in color. At the present time there is a demand for a pale yellow shade to create the illusion that the corn is young. It is extremely important that the corn retain a bright clear color after processing rather than have a grayish or muddy appearance. Such corn is heavily penalized in grading and rated as "standard" or "substandard."

5. *Drought Resistance*

In the Middle West this is one of the most important considerations in a sweet corn breeding program. The high temperature and lack of moisture during critical growth periods require hybrids which have the stamina to produce a satisfactory crop of quality corn.

Haber (1938) found that the reaction of the inbreds to 100°C. temperatures could be used to forecast the performance of hybrids. At such temperatures seedlings of a drought-resistant hybrid survived much longer than seedlings of a drought-susceptible hybrid.

6. *Silk Color*

Within the past few years the importance of silk color inside the husks has engaged the attention of processors. A white or greenish white

silk does not detract from the appearance of the canned or frozen product as is the case with a yellow, tan, or brownish silk. For this reason most sweet corn breeders are giving serious consideration to this character in developing new hybrids.

7. Ear Appearance

Although the appearance of the ear in the husk has no value to the processor, there are certain localities where this character determines the eye appeal and sales value of the product especially from the market gardener's standpoint. Generally speaking the husks should be a good dark green color and the flag leaves well developed. In certain areas market growers demand hybrids which have long flag leaves to serve as a means of identification and differentiation from dent corn.

8. Tillers

With the increased use of mechanical corn pickers there is a growing demand for the reduction or elimination of tillers which tend to clog the machines. For this reason most sweet corn breeders are selecting inbred lines which develop a minimum number of tillers. Such parent lines, however, require careful handling as to date and rate of planting when used as male parents in hybrid seed production. An inbred such as PURDUE 51, which produces several tillers per plant, insures more complete pollination than an inbred having no tillers.

VI. Production of Sweet Corn Seed

During the past 20 years Idaho has become the center of sweet corn seed production, especially the early and midseason yellow hybrids, largely owing to the fact that the land is irrigated and the air is dry enough to reduce or prevent damage from ear rots. Corn-ear worms cause the greatest loss in that area in years of heavy infestation.

Sweet corn is more difficult to mature than dent corn or popcorn, probably owing to its sugary character, and must be harvested before fully mature. This requires special handling and drying to insure satisfactory germination.

Culpepper and Moon (1941) conducted investigations to determine the effect of stage of maturity at time of harvest on the germination of sweet corn seed. Below a certain age germination was progressively poorer the earlier harvesting was done. The grains of ears harvested very early germinated better when allowed to dry on the cob than when removed before drying. Results indicated that ears may be harvested at the proper stage for table use, tests made upon part of the ear to determine its quality, and the remainder dried and preserved for subsequent

planting. This treatment could be carried through three successive generations, thus giving an opportunity for segregating for desirable characters not apparent in the mature grains. Under warm humid conditions such as those found near Washington, D. C., microorganisms attach the seed of ears permitted to dry on the stalk and thus lower the germination. For the production of good seed artificial drying is generally necessary, and the seed should be harvested 35 to 45 days from date of silking or when the dry matter content of the grain has reached 35 to 50 per cent.

Brimhall and Haber (1950) found that dry matter was complete when the moisture level reached 40 per cent during the drying on the stalk. Some hybrids had all their matter at 50 per cent, others at lesser amounts down to 40 per cent. Seed may be harvested when the moisture content of the kernels reaches 40 per cent because there will be no more dry matter to increase the weight or the size of the kernels. If seed is harvested with less dry matter there may be loss in weight and size of seed.

Erwin and Haber (1928) conducted studies on the handling and maturing of sweet corn seed. They found that under field conditions sweet corn releases its moisture more slowly than field corn; this may be due to the sugary character of the endosperm. For this reason producers have adopted kiln drying, which involves the evaporation of the surplus moisture within the seed by means of a current of air, the temperature, humidity, and flow of which are under control. Immature seed may be injured by heat, and it is therefore essential that the temperature used be governed by the maturity of the seed. When the initial moisture content is high, the drying should start at a lower temperature, and this may be increased as the drying progresses. The authors recommended an air replacement of once a minute as a maximum for seed which is very moist and a proportionate reduction for drier seed. Their results indicated that the moisture content of the seed need not go below 15 per cent and that the drying temperature should not exceed 105°F.

Huelsen and Brown (1952) have conducted an extensive study of the physical damage to sweet corn seed during harvesting, drying, and processing. They found that hand-harvested sweet corn suffered the least damage.

No other step in seed processing causes as much damage as shelling. Although there is no corn sheller specifically designed for sweet corn, seedsmen have found that by making certain changes in existing machines and lowering the speed, damage to the seed can be greatly reduced. Shelling at moistures as low as 9 per cent should be avoided.

Processing is a necessary operation in order to put sweet corn into marketable condition, but it is not likely to reduce the percentage of damaged seeds or improve germination. The fanning mill may cause considerable damage in some installations. Sweet corn is inspected over a sorting belt when received at the plant, and in some cases another inspection is made after artificial drying. The equipment varies with each plant, and it is apparent that if the ears are roughly handled, damage and impaired germination will result. Some plants have installed sponge rubber cushions at points where ears might be damaged by striking the sides or bottoms of conveyors.

One of the most serious problems in the commercial production of sweet corn hybrids, especially some of the early types, involves the delayed planting of parent lines. In some cases there are instances where the difference in planting dates may be as much as three to four weeks. This requires careful study of the weather during the intervening period to insure proper pollination when the silks are receptive.

The use of line crosses between sister lines of the seed parent has become an important part in the production of hybrid sweet corn seed. More effort should be made to find out which are the best line crosses. Singleton (1948) maintains that all the existing sublines of an inbred such as PURDUE 39 should be tested to see which combination produces the most productive and desirable line cross. Preliminary results indicate that the better sublines will produce the better line crosses, and there are theoretical grounds to believe that the best line crosses would give the superior hybrids when crossed by unrelated lines.

Haber (1950) investigated the longevity of seed of sweet corn inbreds and hybrids and found a wide difference when the seed was stored under the same conditions. Some inbreds had high germination after seven years of storage, whereas others dropped in germination in three years. This was also true of hybrid seed. He found that when two long-lived inbreds were crossed the resulting hybrid seed was long-lived, and similarly the hybrid seed from two short-lived inbreds lost germinability in a short time.

VII. Present-Day Hybrids

An attempt to list present-day hybrids would be of little lasting value because so many new varieties are introduced each year that within a short time such information would be out of date. However, several hybrids have stood the test of time and may be expected to continue in favor for a few more years. Some have been developed and released by state experiment stations and some by commercial seedsmen. Table I adapted from Boswell (1952) represents only a small portion

of those now on the market. Each year new varieties are introduced, and many will undoubtedly be popular in the future.

TABLE I
POPULAR PRESENT-DAY HYBRIDS (ARRANGED ACCORDING TO SEASON)

<i>Variety</i>	<i>Originator</i>	<i>Pedigree</i>	<i>Kernel color</i>	<i>Ear length inches</i>	<i>Kernel rows number</i>
<i>Early Types (65 to 74 Days to Harvest)</i>					
SPANCROSS	Conn. A.E.S.	C13 × C3	Yellow	6½	10-12
NORTH STAR	Joseph Harris Co.	Closed	Yellow	6½	8-12
MARCROSS	Conn. A.E.S.	C13 × C6	Yellow	7½	10-14
SENECA 60	Robson Seed Farm	Closed	Yellow	6½	10-12
<i>Early Midseason Types (75 to 80 Days to Harvest)</i>					
CARMELCROSS	Conn. A.E.S.	P39 × C13	Yellow	7	12-14
GOLD RUSH	Corneli Seed Co.	Closed	Yellow	7	12-14
<i>Midseason Types (81 to 89 Days to Harvest)</i>					
LINCOLN	Conn. A.E.S.	P39 × C23	Yellow	7½	12-16
GOLDEN BOUNTY	Northrup King & Co.	Closed	Yellow	8	10-14
F M CROSS	Ferry Morse Co.	Closed	Yellow	8	12-14
GOLDEN CROSS BANTAM	Purdue A.E.S.	P39 × P51	Yellow	8	12-14
IOANA	Iowa A.E.S.	P39 × I45	Yellow	8	12-14
SENECA CHIEF	Robson Seed Farm	Closed	Yellow	9	12
ERIE	Assoc. Seed Growers	Closed	Yellow	9	12-14
ARISTOGOLD BANTAM					
EVERGREEN	Michael Leonard Co.	Closed	Yellow	9½	16-18
ILLINOIS GOLDEN NO. 10	Ill. A.E.S.	101q × 73c	Yellow	7½	12-14
GOLDEN SECURITY	F. H. Woodruff & Son	Closed	Yellow	8	14-16
VICTORY GOLDEN	F. H. Woodruff & Son	Closed	Yellow	8	16
IOCHIEF	Iowa A.E.S.	5125 × 453	Yellow	9	16-18
<i>Large Late Types (90 Days or Over to Harvest)</i>					
EVERGREEN 14 × 11	Ill. A.E.S.	14 × 11	White	8	16-20
COUNTRY GENTLEMAN 13	Ill. A.E.S.	27a × 18b	White	7½	Irreg.

REFERENCES

- ANONYMOUS. 1939. *Maine Agr. Expt. Station Rept. Progr.*
 ANONYMOUS. 1939. *Wisconsin Agr. Expt. Sta. Bull.* **443**: 53.
 ANONYMOUS. 1953a. *Market Growers J.* **82** (No. 7), 9.
 ANONYMOUS. 1953b. *Market Growers J.* **82** (No. 8), 21.
 APPLEMAN, C. O., and ARTHUR, J. M. 1919. Carbohydrate metabolism in green sweet corn during storage at different temperatures. *J. Agr. Research* **17**: 137-152.
 BAILEY, D. M., and BAILEY, R. M. 1938. The relation of the pericarp to tenderness in sweet corn. *Proc. Am. Soc. Hort. Sci.* **36**: 555-559.
 BEATTIE, J. H. 1936. Growing sweet corn for the cannery. *U. S. Dept. Agr. Farmers' Bull.* **2024**.
 BOSWELL, V. R. 1952. Commercial growing of sweet corn. *U. S. Dept. Agr. Farmers' Bull.* **1634**.

CHAPTER XII

Diseases of Corn

ARNOLD J. ULLSTRUP

I. Introduction

Corn is subject to a number of infectious diseases which annually reduce yield and quality of the crop. Conservative estimates indicate that yearly losses in the United States, as a whole, may range from about 2 to 7 per cent. In some fields the damage caused by disease may greatly exceed these estimates. The diseases of corn, unlike some affecting other crops, seldom are very destructive over wide areas. The production of corn has not been limited by disease where weather and soil are favorable for the crop, nor has its culture been forced to move to new localities because of diseases. Precise, quantitative data of the effects of diseases on corn yields are difficult to obtain. A few of the situations which confront any attempt at accurate determination of disease losses and which contribute to the difficulty of arriving at reliable estimates, may be mentioned: Reduction in stand due to seedling blights cannot be interpreted directly as yield loss. Plants in thinned stands may compensate to some extent for the lower population. The amount of compensation, however, may depend on soil fertility and moisture. Where these are in short supply compensation tends to be greater than where plant food elements and soil moisture are ample. The amount of leaf area killed by diseases may not always indicate a corresponding loss in yield. The time of onset of leaf diseases is very important in determining how much yield will be reduced. Leaf diseases that become severe after ears have attained the maximum amount of dry matter cause little if any yield reduction. Where leaf infections become severe at silking or shortly after, yields may be lowered by as much as 50 per cent. In only a few instances have the economic losses due to a specific disease been accurately measured.

1. Factors Affecting Disease Development

Fluctuation in severity and prevalence is a characteristic of most plant diseases. This variation depends on three important factors, namely, the environment, the presence or absence of the often variable

disease-inciting agent, and the relative resistance or susceptibility of the host. Epiphytotics occur when these three factors are favorably balanced and act co-ordinately. The absence or failure of one factor may upset this balance and check disease development. Thus the environment may be optimum for a particular disease and the specific pathogen may be present, but if the host is resistant, an epiphytotic will not occur. Or, the pathogen may be present and the host susceptible, but an unfavorable environment may preclude any disease development. The shift in the relationships between these factors determines largely the variations commonly observed in the prevalence and severity of plant diseases.

a. Environment. Temperature, rainfall, and humidity have a marked influence on diseases of plants. Fertility, drainage, and pH of the soil may play an indirect but certain role. Although the environmental requirements may differ for the various diseases of corn, many are favored by ample supplies of moisture and moderate temperatures such as are generally considered to be optimum for growth of the host. Free moisture on the surface of the plant is necessary for germination of spores of the fungi that attack corn. Some diseases such as pythium stalk rot and brown spot are favored by comparatively high temperature and moisture conditions. Northern corn leaf blight and common corn rust thrive under more moderate temperatures and heavy dews. Seedling blights are most severe when extended periods of cold wet weather follow planting. Diplodia stalk rot is often more prevalent when the supply of potassium is low. Crazy top of corn occurs only where drainage is poor and soil is apt to become waterlogged.

b. Host Resistance. The inherent resistance or susceptibility of a corn hybrid may be a determining factor in the occurrence of disease. Hybrids exhibit marked differences in resistance to certain diseases. Resistance or susceptibility to most of the common diseases of corn is determined by a number of genes. So far as is known at present, in only two diseases is resistance inherited as a monogenic dominant. Most of the currently used and widely adapted hybrids show reasonable resistance to the more important diseases under mild epiphytotics. When certain diseases attain moderate-to-severe proportions, these hybrids may sustain appreciable injury. This is particularly true in seasons when some of the leaf blights or stalk rots are prevalent, because most of the hybrids grown are susceptible to at least one of the leaf blights, and many do not possess as high a level of resistance to stalk rot as is desired. Within the past 10 to 15 years breeding programs have been started by the United States Department of Agriculture and some of the state agricultural experiment stations for the purpose of developing hy-

brids resistant to some of the more important corn diseases. The progress made thus far offers promise that much improvement can be made in developing hybrids of high resistance to the major diseases in a given area while maintaining the yielding ability and other desired agronomic qualities now possessed by some of the more popular hybrids.

Disease resistance is only one of the many characteristics sought in a corn hybrid, and it may be difficult to find all the wanted qualities in any one hybrid. In areas where certain diseases often measurably reduce yield, greater consideration must be given to disease resistance.

c. The Disease-Inciting Agent. Most diseases of corn are caused by fungi, a few by bacteria, and a few by viruses. The majority of these diseases occur in the United States. Some of the downy mildews, some of the more serious virus diseases, and tropical rust are examples of corn diseases that are not found in this country. Exclusion of some of these diseases may be due to an unfavorable environment affecting the disease-producing agent directly or the insect vector indirectly, as in the case of viruses. Quarantine measures have played an important role in keeping some diseases from entering this country.

Variability in pathogenicity is often encountered in plant disease organisms and viruses. This variation may originate as a result of combination and segregation of genetic factors for pathogenicity following sexual fusion between compatible biotypes within a species, by mutation, or by somatic segregation of nuclei in heterocaryotic species. The occurrence of specialized pathogenic races within species of disease-producing organisms may be accounted for on these bases. A well-known instance of the advent of new races is that found within the species of rust fungi attacking small grains. These changes in pathogenicity of disease organisms have complicated the work of the plant breeder in many instances. A variety resistant to a particular disease may be developed which subsequently succumbs to the attack of a new race of the disease-inciting organism. Among those organisms producing diseases in corn, physiologic specialization is known to occur in some of the rust and smut fungi. Thus far, in breeding for resistance to some of the leaf blights and stalk rots, the problem of specialized pathogenic races has not arisen.

2. Control of Corn Diseases

Two important means of combatting corn diseases are: (1) the use of resistant hybrids, and (2) the application of fungicides to the seed.

Planting genetically resistant hybrids is the most certain and long-lasting way of preventing disease losses. No single hybrid is resistant to all diseases and whether one could be developed or is even necessary, is

questionable. Hybrids of reasonable resistance to the major diseases that may occur over rather wide areas can be produced by breeding procedures. In general the resistance of a hybrid to a given disease is proportional to the number of resistant inbred lines in its pedigree. Thus, when four resistant inbred lines are combined, the double-cross hybrid will be resistant to the disease in question. A hybrid made up of four susceptible inbred lines will generally show high susceptibility. In some cases dominance of resistance or susceptibility to a particular disease or the interaction of genetic factors may complicate or upset this general relationship. Much remains to be accomplished in developing hybrids resistant to different diseases.

The use of fungicides as seed-treating materials is limited to the control of seedling blights. So far as is known other corn diseases are unaffected by this practice. Considerable advancement has been made in improving corn seed treating materials. Excellent seed treatment preparations are now available, and most of the seed corn sold at present is treated with some fungicide.

Other control measures may be mentioned which are less important, are limited in their use, or have had insufficient testing to warrant general recommendation. Spraying plants with fungicides has been successful in reducing certain leaf diseases of sweet corn in Florida. This appears to be economically feasible on a high-value crop such as market garden sweet corn in certain areas where leaf diseases are often quite destructive. Limited spraying trials have been conducted in seed fields of hybrid dent corn in the Corn Belt for the control of northern corn leaf blight, but whether this practice will become general awaits further testing.

Building up and maintaining well-balanced soil fertility has been recommended as a means of reducing corn diseases. Observations have indicated that some diseases, such as diplodia stalk rot, are less severe where major plant food deficiencies have been corrected and fertility of the soil restored to proper balance. Recommended soil management practices certainly are beneficial and will tend to produce maximum, economic yields. There is need for more evidence from experiments designed specifically to determine the relationship of soil fertility to disease control in corn. At present the general statement cannot be made that all diseases of corn can be prevented or reduced by increasing soil fertility.

Crop rotation and sanitation measures, such as clean plowing and destruction of diseased plant refuse, have been cited as ways of reducing corn diseases. Where corn is grown extensively over wide areas there is some doubt if these practices would be effective means of disease

control. Crop rotation is probably more beneficial in improving soil fertility and tilth than in reducing corn diseases. Destruction of disease-harboring crop refuse is hardly practical where many thousands of acres of corn are grown.

II. Seed and Seedling Diseases

Seed rot and seedling blight may often be responsible for reduced stands of corn. Seed rot and seedling blight are not necessarily distinct diseases, the terms implying only differences in severity of infection. Severe infection that takes place soon after planting may destroy the embryo before germination. Blighted seedlings may be destroyed before or after emergence, or may survive and develop into productive plants. The incidence of seed decay and seedling blight varies from year to year and is generally, but not always, greatest when soil temperatures are too low to permit rapid germination and growth of corn.

Symptoms of seedling blights vary with the particular pathogen involved (Fig. 1). All virulent seedling blight fungi are capable of completely rotting the entire seed before germination. Lesions of varying extent may be formed on the roots, the mesocotyl, and the coleoptile. The lesions may be water-soaked, flaccid, or sunken, and variously discolored. Because of the variation in symptoms it would be difficult to classify blighted seedlings according to inciting agents, entirely on the basis of symptoms. The species of *Pythium* found on corn seedlings often attack the roots, but they can invade the mesocotyl or cause seed rot before germination (Johann *et al.*, 1928). Seedlings infected by *Gibberella zeae* and *Diplodia zeae* show conspicuous lesions on the mesocotyl (Dickson, 1923; Johann *et al.*, 1923). Wilting and drying of leaves is a characteristic symptom of seedlings attacked by *Penicillium oxalicum*. Koehler and Woodworth (1938) have described a distinctive virescence of seedling leaves following infection by *Aspergillus flavus* and *A. tamarii*. Pronounced stunting of seedlings was observed by Hoppe (1949) following inoculation, at soil temperatures of 20° to 24°C., with an undetermined species of *Pythium*. The same isolate caused complete seed decay at a soil temperature of 11°C.

A large number of fungi have been shown capable of inciting seed decay or seedling blight of corn. Some of the most important are species of *Pythium* (Johann *et al.*, 1928; Hoppe and Middleton, 1950; McKeen, 1951a; Hooker, 1951). These are soil-borne and are generally most destructive at comparatively low soil temperatures where the host is unable to grow and compete favorably with the pathogen. Hoppe and Middleton (1950) have pointed out the difference in virulence between the species of *Pythium* isolated from seedlings grown in various

soils in Wisconsin. The population of *Pythium* species varied both quantitatively and qualitatively with soil type and crop sequence.

Most of the fungi causing typical ear rots also invade seedlings. When these fungi become established in kernels before harvest, they



FIG. 1. Seedling blight showing a range in severity of infection.

will frequently continue to invade and kill the embryo or young seedling after planting. *Gibberella zeae* and *Diplodia zeae* are two of the most virulent of seed-borne pathogens. *Nigrospora oryzae* becomes actively parasitic when infected seed is planted in cold soil where germi-

nation is suppressed. Under conditions favoring rapid germination infected seed will produce vigorous seedlings. According to Reddy (1933) the embryo becomes resistant to invasion by *N. oryzae* by virtue of an increase in acidity in the tissues when germination is initiated. Seedling blight caused by *Penicillium oxalicum* is most destructive at soil temperatures ranging between 24° and 28°C. (Johann *et al.*, 1931). Diachun (1939) reported this disease to be more severe in dry than in wet soils. Johann *et al.* (1931) consider *P. oxalicum* to be essentially saprophytic and unable to invade vigorous living cells. Penetration of the host tissue occurred only after the latter had been killed by oxalic acid produced by the fungus. The virulence of *Gibberella fujikuroi* (*Fusarium moniliforme*) seems to be questionable. Valteau (1920), Voorhees (1933a), and Edwards (1935) consider the fungus to be an active pathogen on corn seedlings. Limber (1927), Leonian (1932), and McKeen (1951b) are of the opinion that the fungus is a weak parasite and largely a secondary invader. In the experience of the writer neither *G. fujikuroi* nor *G. fujikuroi* var. *subglutinans* has ever shown active parasitism on corn seedlings or stalk tissue. Stover (1922) and Davidson (1950) have reported several species of *Helminthosporium* capable of inciting seedling blight; and Semeniuk (1944) has shown that *Sclerotium bataticola* may become pathogenic on corn seedlings. These fungi appear to be of lesser importance than those mentioned above.

Control of seedling diseases can be effected by avoiding conditions that predispose the seed and seedling to infection and by using practices that afford protection from pathogens. The use of mature, well-finished seed is one means of avoiding these tissues. It has been shown that fully matured kernels make more rapid and vigorous growth and are less susceptible to invasion by soil-borne fungi than immature kernels (Koehler *et al.*, 1934; Rush and Neal, 1951). The soundness of seed is an important factor in determining susceptibility to seed decay and seedling blight. Kernels injured during seed-processing operations are more apt to become infected by fungi than sound seed (Alberts, 1927; Koehler, 1935). Studies by Tatum and Zuber (1943) have pointed out that breaks in the seed coat over the germ are more critical than those on other parts of the kernel. Significant reductions in stand and yield resulted from the use of such seed. Care in processing operations and proper adjustment of shelling machinery tend to minimize such abrasions.

Treatment of seed corn with an effective fungicide is one of the simplest ways of protecting the seed and seedling from invasion by soil-borne fungi. The benefits from seed treatment are almost always

greatest when immature, injured seed is used and when cold weather follows planting. Delay in planting of corn until danger of extended periods of cold weather has passed is another means of reducing the seedling disease hazard.

Cold testing of seed corn in the laboratory has attracted interest in recent years as a possible tool in (1) determining the germinability of seed lots under conditions simulating the adverse environments that sometimes prevail in the field, (2) detecting the effectiveness of seed treatment preparations, (3) evaluating seed processing procedures in relation to pericarp injury, and (4) indexing inbreds and hybrids with respect to genetic resistance to seed rot and seedling blights. Hoppe (1951, 1952) and others have developed methods for cold testing seed corn in the laboratory. The methods consist essentially of placing seed in contact with moist field soil for 7 to 10 days at about 50°F. Following this treatment the seed is placed at about 80°F. and germination recorded after 3 to 7 days. The objectives and procedures in cold testing have been reviewed by Isely (1950) and Wernham (1951). In the experience of the writer cold testing of disease-free seed in a sterile medium, such as moist autoclaved sand or vermiculite, has given essentially the same results as conventional germination tests run at temperatures optimum for germination. When replicates of the same seed were cold tested in field soil, germination was often reduced considerably. This suggests that cold testing is a means of detecting resistance to invasion by pathogenic fungi and not resistance to low temperatures *per se*. Seed treated with a good fungicide generally shows higher germination following the cold test than untreated seed. This is further evidence that the cold test is a means of determining resistance to disease; fungicides do not protect seed from cold. Inbred lines vary in ability to germinate at low temperatures, and this may bear some relation to their resistance to disease.

Breeding for resistance is a possible means of controlling seedling diseases, but thus far comparatively little has been done on this aspect of the problem. Inheritance of resistance to seedling diseases is complex and determined by a number of genes. In view of the number of pathogens involved it is questionable whether the genetic factors determining resistance to infection by one fungus would govern also resistance toward all others. Hoppe (1929) found a wide range of resistance among inbred lines to seedling blight incited by *Gibberella zeae*. The behavior within inbred lines was consistent, and in hybrids there was some indication of dominance of resistance. Some F₃ families were more resistant than the most resistant parent; other progenies were more susceptible than the most susceptible parent. McIndoe

(1931) concluded that resistance to infection by *G. zeae* was conditioned by a number of genes. In a study of the reaction of maize seedlings to *G. zeae*, Hayes *et al.* (1933) found consistent behavior in replicates obtained from the same ear, but interannual variation within inbred lines was high. They concluded that the environment under which an ear develops determines to a considerable degree the reaction of the progeny to seedling blight. Leng (1949) found wide and consistent differences among inbred lines in resistance to *Penicillium oxalicum*. High resistance was less frequently observed than extreme susceptibility. Some inbreds were variable in reaction, but this was attributed to degree of maturity and age of seed rather than to genetic variation within the inbred lines.

III. Stalk and Root Rots

Diseases of stalks and roots of corn are widespread and often responsible for appreciable yield losses. When they become established before full maturity, ears are chaffy. Much of the lodging in corn is caused by these diseases. Broken and down stalks are difficult to harvest, and ears in contact with moist soil are soon destroyed by fungi.

The distinction between stalk rots and root rots is not always clear-cut. Some of the fungi associated with stalk rots are capable also of invading and destroying the roots, but others appear to be confined only to stalk tissue and make little advance into the roots. *Pythium* root rot seems to be limited to roots only. Most of the stalk rots become active as the host approaches maturity.

A number of fungi and bacteria have been isolated from diseased stalks and roots. The pathogenicity of some of these organisms has been fully established; in other cases definite proof of the disease-inciting capabilities of the isolates is lacking. Those diseases of stalks and roots in which the pathogenicity of a specific inciting agent has been proved are described below.

1. *Diplodia* Stalk Rot

Diplodia stalk rot is a common disease and is probably responsible for more premature killing of plants and stalk breakage than any of the other diseases attacking corn stalks.

The disease does not ordinarily become apparent until several weeks after silking. Affected plants die suddenly, and their leaves take on a dull grayish green cast resembling frost injury. Lower internodes are brown to straw-colored, spongy, and easily crushed (Fig. 2A). The pith disintegrates rapidly leaving only the vascular bundles intact (Fig. 2B). Plants that are killed prematurely produce chaffy, poorly finished

ears. The amount of stalk breakage following attacks by this disease is always greater when high winds and driving rains are prevalent in the fall. When diplodia stalk rot is delayed until plants are mature, little if any yield reduction occurs, but the hazard of stalk breakage remains. Roots of plants attacked by this disease usually show discoloration and disintegration. A definite sign of diplodia stalk rot is the presence of black pycnidia of the fungus on the stalk. Pycnidia are subepidermal and most abundant near the nodes (Fig. 3A). In some years they are numerous in the fall, whereas in others their development is delayed until the following spring.

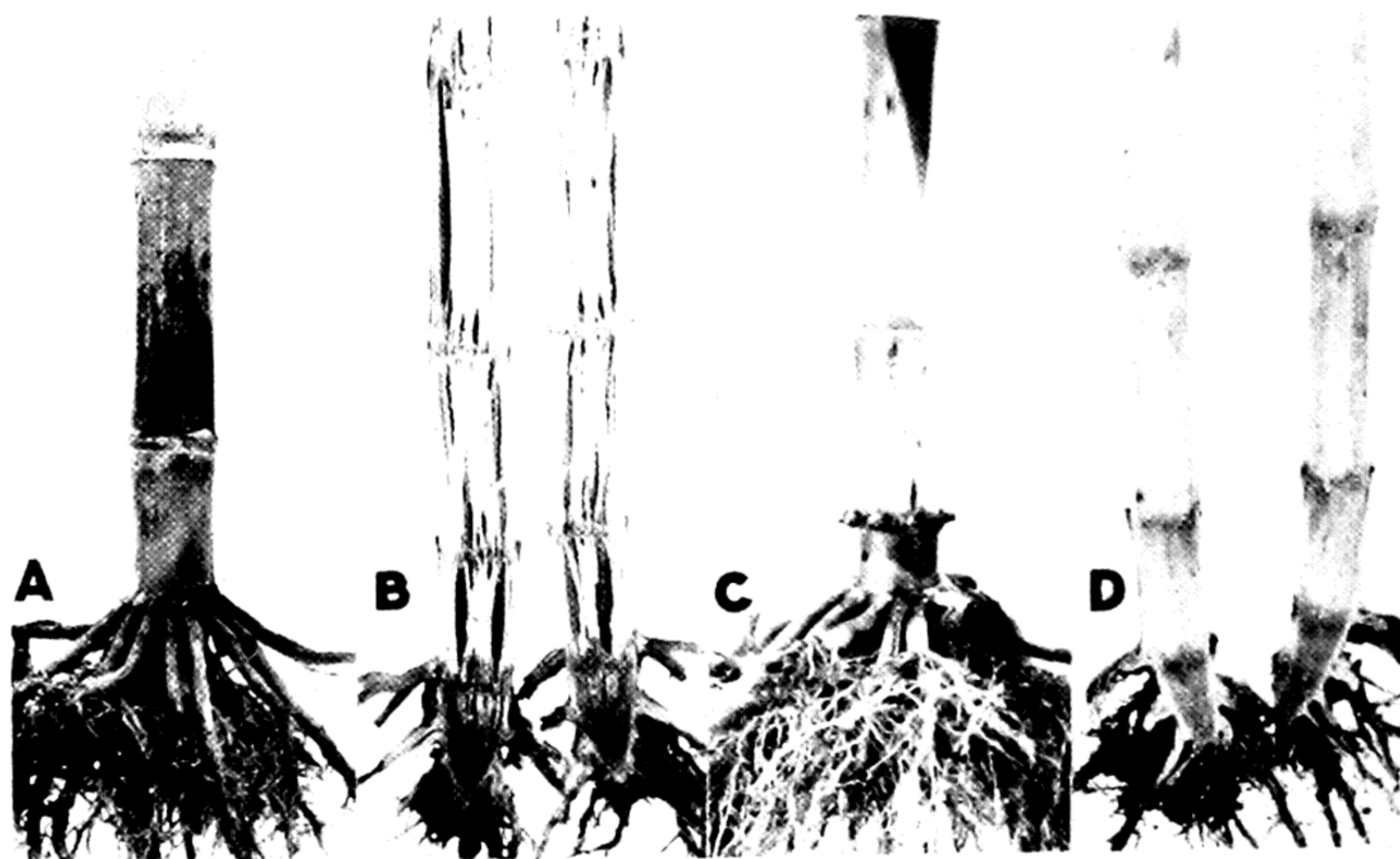


FIG. 2. Diplodia stalk rot. *A*. External appearance of an infected stalk showing discoloration and early development of pycnidia of the fungus. *B*. Infected stalk split open to show shredded condition of the pith. *C* and *D*. Healthy stalks—external and internal appearance.

Diplodia stalk rot is incited by *Diplodia zeae*. The fungus produces two kinds of spores. The most commonly occurring type is olivaceous to brown, long-oval, straight to slightly curved, generally two-celled, and $25\text{--}30 \times 5\text{--}6 \mu$ in size. The second type, which has only recently been found (Johann, 1939), is hyaline, threadlike, and $25\text{--}35 \times 1\text{--}2 \mu$ in size. Both spore types are borne in black pycnidia which develop on infected parts of the host. Under warm moist conditions spores are exuded from the pycnidia and thence dispersed by wind. No sexual stage of the fungus is known.

Infection of stalks may take place at the nodes following germination of spores of the fungus that lodge behind leaf sheaths (Durrell, 1923). According to McNew (1937a), initial infection occurs in the seedling stage. The pathogen, which may be in the soil or in the seed, invades the mesocotyl or the crown of the young plant. Such seedlings,

once they have established adventitious roots, do not die, but remain parasitized during the remainder of the growing season. The progress of the fungus is limited until sometime after pollination when, with the lessening of physiological activity that accompanies the approach of maturity, the quiescent infection becomes active and lower internodes of the stalk are invaded. Although the fungus traverses some distance from the crown to lower internodes, diplodia stalk rot is not a systematic



FIG. 3. A. Pycnidia of *Diplodia zeae* on a diseased stalk. B. Perithecia of *Gibberella zeae* on an overwintered infected stalk. Perithecia are superficial; pycnidia of *D. zeae* are subepidermal.

disease in the general sense of the term. Observations suggest that most infection progresses from the crown into the stalk, but local infections at the lower nodes also occur. There is some question whether diplodia-infected seed is a major source of infection. The low percentage of diplodia-infected kernels found by the writer on pathological examination of seed samples over a period of several years does not correlate closely with the prevalence of diplodia stalk rot during this period.

A number of factors affect the prevalence and severity of diplodia stalk rot. Although the epiphytology of the disease is not fully known, it has been observed that wet weather in August and September is conducive to the development of this disease. This seems to be especially

so if the rainy period is preceded by unusually dry weather in June and July.

Soil fertility appears to have some influence on the severity of diplodia stalk rot. Hoffer and Carr (1923) suggested that the accumulation in the corn plant of toxic concentrations of iron and aluminum salts predisposes the stalks to invasion by *Diplodia zeae* and other stalk- and root-rotting organisms. When toxic amounts of these salts were found in stalks, the soil often indicated a deficiency of phosphorus. Applications of lime and phosphate tended to reduce the severity of stalk and root rots. In light of McNew's (1937a) studies, the accumulation of iron and aluminum compounds in stalk tissues may have been a result of crown infection that took place early in the life of the plants and not a factor that predisposed them to invasion. It is not clear whether the occurrence of these toxic metallic salts in stalks was a cause or an effect of stalk and root rotting. Koehler (1950) pointed out that low levels of potassium in the soil aggravate the severity of diplodia stalk rot, but that the disease may be favored also by high levels of nitrogen in the soil. He suggests that in soils of well-balanced fertility the disease is apt to be less severe.

Holbert *et al.* (1935) have shown that the severity of diplodia stalk rot increases when the functional leaf area is reduced. If leaf tissue was killed by leaf blights or low temperatures, or removed by clipping, stalk rot became worse. They concluded that any condition that reduced carbohydrate reserves in the stalk increased susceptibility to diplodia stalk rot. Prevention of fertilization by removing ears or protecting silks from pollen, which presumably increases carbohydrate reserves in the stalk, decreases susceptibility to stalk rot.

Differences in resistance to diplodia stalk rot occur among inbred lines and among hybrids. Early maturity is often associated with susceptibility. There are, however, exceptions to this generally observed relationship, whereby certain comparatively early-maturing inbred lines are more resistant than some that mature later. These exceptions suggest that physiological factors, other than those that may be associated with relative maturity, play a part in determining resistance. Control of diplodia stalk rot has been accomplished in part by selection and use of resistant inbred lines in hybrid combinations. Resistance to the disease is probably determined by a number of genes.

The nature of resistance was investigated by Johann and Dickson (1945). They found that ether extracts of stalk tissue collected soon after pollination inhibited growth of *Diplodia zeae* in pure culture to a greater degree than did ether extracts from stalk tissues collected later in the season. This correlates with the general trend of susceptibility of

stalks to invasion at such periods. Prevention of pollination or artificial defoliation, however, did not increase or decrease the growth-retarding effects of ether extracts made from stalks of plants so treated. Magee (1948) studied the histological structure of stalks in relation to susceptibility to breakage. In the materials used, stiff-stalked inbred lines had greater stalk diameter, thicker cell walls in the epidermis, a lower number of vascular bundles in the "rind," and a higher percentage of sheath per bundle than did weak-stalked inbred lines. Exceptions were observed wherein a stiff-stalked inbred line did not differ morphologically from a weak-stalked line. It was suggested that resistance to stalk breakage may involve both morphological and physiological factors.

2. *Gibberella Stalk Rot*

Gibberella stalk rot is widely distributed but appears more frequently in the northern and eastern parts of the Corn Belt. The incidence of the disease varies from year to year, and only occasionally is it more prevalent than diplodia stalk rot.

The symptoms of the disease are similar to those of diplodia stalk rot. Lower internodes are brown to straw-colored and the pith is disintegrated. Pink-to-reddish discoloration of the pith distinguishes this disease from diplodia stalk rot, although this characteristic may not always be present.

Gibberella zeae is the inciting agent of the disease. Perithecia are black, spherical, and borne on the surface of diseased parts of the plant. Perithecia may form on the stalks in the fall but usually do not mature until warm moist weather prevails during the following spring (Fig. 3B). Asci develop within the perithecia and each contains 8 ascospores. The ascospores are hyaline, long-oval in shape, 1–3 septate, and $20\text{--}30 \times 3\text{--}5 \mu$ in size. Mature ascospores are exuded from the perithecia during warm humid weather and are dispersed by wind to susceptible host plants, where they germinate and penetrate the tissues. Spores of the asexual stage of the fungus (*Fusarium graminearum*) are hyaline, slightly curved with pointed ends, 3–5 septate, $30\text{--}60 \times 4\text{--}6 \mu$ in size, and borne on the mycelium.

The factors influencing prevalence of the disease are essentially the same as those affecting diplodia stalk rot. Differences in resistance are evident between inbred lines. The mode of inheritance of resistance has not been determined, but probably a number of genes are involved.

3. *Charcoal Rot*

Charcoal rot is found in the drier areas where corn is grown (Livingston, 1945; Hoffmaster *et al.*, 1943). Mackie (1932) described the

disease on corn and other crops in the Sacramento Valley of California. In some years the disease has extended into the central parts of the Corn Belt (Tehon and Boewe, 1939; Semeniuk, 1942).

Symptoms first become apparent as plants approach maturity. Affected plants show evidence of premature ripening and often break over



FIG. 4. Charcoal rot of corn. (Courtesy of J. E. Livingston, Nebraska Agricultural Experiment Station.)

at the crown. The outside of the lower internodes may become dark-brown, but more often they are straw-colored. The pith, which generally shows little discoloration, becomes badly disintegrated (Fig. 4). A distinguishing sign of the disease is the presence of numerous small black sclerotia scattered in the pith of affected stalks. Roots are also invaded and show black sclerotia in the disorganized tissues.

Macrophomina phaseoli (*Rhizoctonia bataticola*, *Sclerotium batati-*

cola) is the inciting agent. The fungus has a wide host range and appears to be composed of a number of forms which are differentiated on the basis of size of sclerotia and the presence or absence of pycnidia. The form attacking corn does not produce pycnidia in nature. Ashby (1927) and Haigh (1928) studied the fungus from the standpoint of the relationship of pycnidial forms to sterile forms which produce only sclerotia. Spores are hyaline, oval, unicellular, $12-30 \times 6-12 \mu$ in size, and borne in black, flask-shaped pycnidia. Sclerotia are black, irregular to globular in shape, and range from $\frac{1}{20}$ to $\frac{1}{5}$ mm. in diameter.

Soil temperature and moisture are important factors determining the severity of the disease. Livingston (1945) has found the disease most severe in dry soils where the temperature was held at about 38°C .

No information is available regarding the reaction of different inbred lines to the disease, although Semeniuk (1944) found differences in response of inbred lines to the seedling phase of the disease.

4. *Pythium Stalk Rot*

Pythium stalk rot is a comparatively recently recognized disease in the United States. Elliott (1943) first described the disease in Virginia; since then it has been found in a number of localities in the eastern half of this country. The disease is probably present in Europe (Curzi, 1929); and Pontis-Videla (1951) has described it in Venezuela.

The presence of the disease is usually first recognized when plants fall over. Stalks show a rotted area near the soil line (Fig. 5). Tissues in the rotted portion, which seldom extends beyond one internode, are brown, soft, and disintegrated; only the vascular bundles remain intact. A sharp line of demarkation separates the diseased from the healthy tissue. When plants fall over they frequently continue to live for some time and may develop roots at nodes above the rotted area. Plants may be attacked at any stage of development, but roots generally are not invaded.

The inciting fungus has been identified as *Pythium butleri*. Hyphae are hyaline, and nonseptate except near fruiting structures. Sporangia are filamentous, inflated, branched or unbranched, and $50-1000 \mu$ in length $\times$ $4-20 \mu$ in width. Zoospores, borne in the sporangia, are reniform, biciliate and $12 \times 7.5 \mu$ in size. Oögonia are usually terminal, spherical, and $22 \times 27 \mu$ in diameter. Antheridia are either terminal or intercalary, 1 to 2 per oögonium, barrel-shaped, and $9-11 \times 10-14 \mu$ in size. Oöspores are thick-walled and $17-19 \mu$ in diameter, germinating by the production of a germ tube. *P. butleri* and *P. aphanidermatum* are very similar morphologically, and the latter has sometimes been identified as the inciting agent of *pythium stalk rot*. Dreschler (1934a)

maintains that the two species are separable on the basis of larger zoosporangia and sexual structures in *P. butleri*. Middleton (1943) is of the opinion that *P. butleri* is a synonym of *P. aphanidermatum*.

The disease becomes destructive only when temperature and humidity are abnormally high over a period of 10 to 14 days. This disease

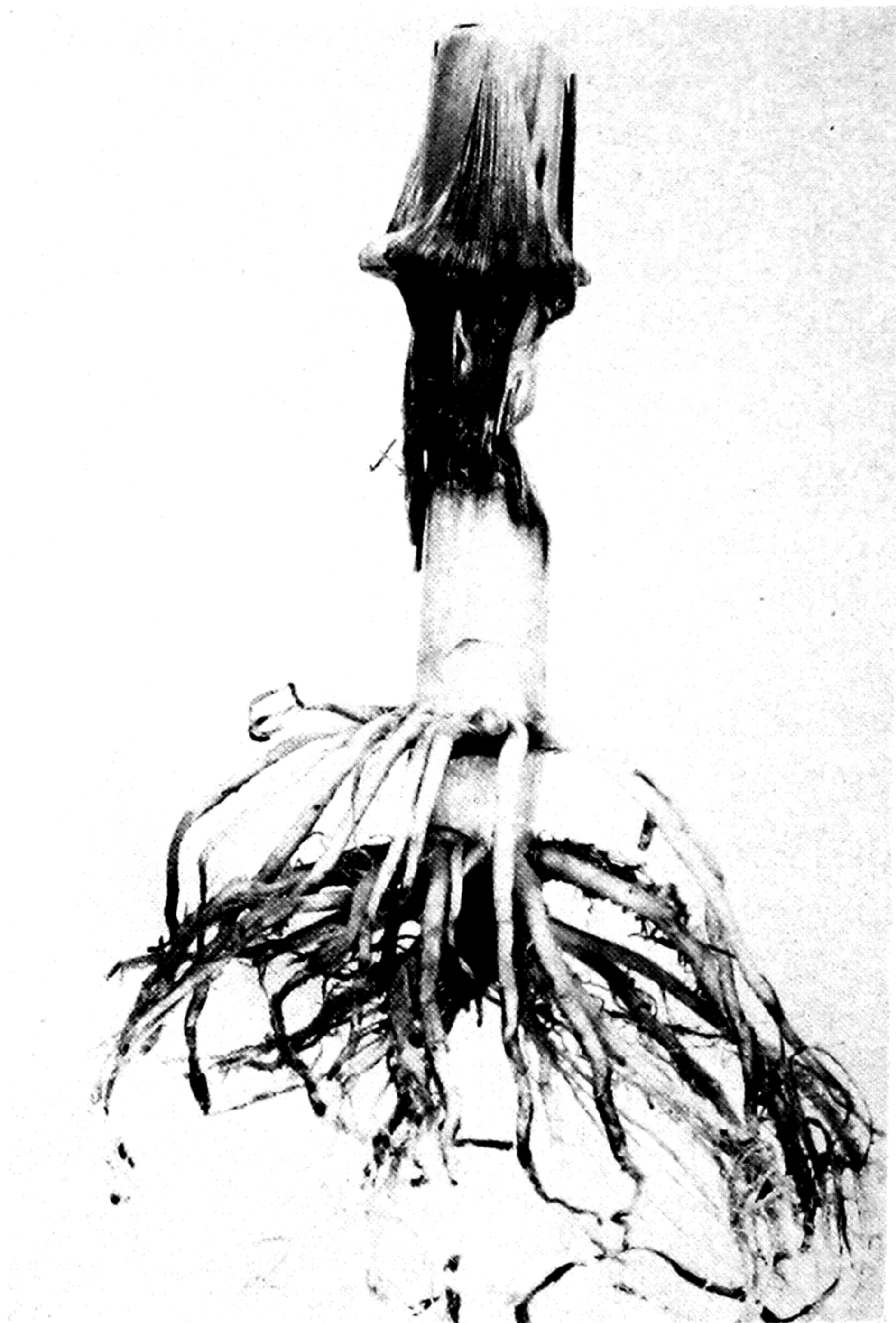


FIG. 5. Pythium stalk rot. Rotted area is brown, tissues disintegrated, leaving only vascular bundles intact. The lesion is restricted and seldom extends beyond one internode.

differs from the stalk rots previously described in that it attacks green stalks of vigorously growing plants.

Elliott (1943) found differences in resistance among inbred lines under conditions of natural infection in the field and also in the greenhouse when plants were artificially inoculated.

5. *Pythium* Root Rot

Pythium root rot of corn appears to be widely distributed over the Corn Belt (Valleau *et al.*, 1926; Branstetter, 1927), but is evidently not so destructive on this crop as on sugar cane, sorghum, and related plants.

The disease attacks the small feeding roots primarily. Infected roots are yellowish to brown and flaccid. Invasion often takes place at root ruptures. In later stages of development the entire root system and crown tissues may be involved. Plants may be attacked at any stage of development. Root lodging often follows severe attacks by this disease.

Pythium root rot may be incited by a number of species of *Pythium*. *P. arrhenomanes* (Dreschler, 1928) and a closely related species *P. graminicolum* have been frequently isolated from corn roots showing symptoms of the disease. Ho (1944) found *P. debaryanum* to be one of a number of fungi isolated from diseased corn roots. The species of *Pythium* isolated from corn roots are differentiated on the basis of size, shape, and arrangement of asexual and sexual structures (Middleton, 1943). Rands and Dopp (1934) studied the variability of *P. arrhenomanes* and concluded that the species is composed of a number of variously differentiated forms. The species of *Pythium* isolated from corn roots attacked by this disease have a very wide host range.

Pythium root rot often becomes severe when soil is cold and wet and poorly drained. Elliott (1942) has shown that some inbred lines differ in resistance to this disease.

6. Other Stalk Rots

A bacterial stalk rot and the inciting organism were described by Rosen (1922a) in Arkansas. The disease was reported later in West Virginia by Stanley and Orton (1932). Rotting of the stalk occurs near the soil line and seldom progresses for more than one internode. The infected parts are brown, soft, and disintegrated, with a disagreeable odor. Badly infected plants fall over at the point where the stalk is rotted. The symptoms of this disease and *pythium* stalk rot are virtually identical. The distinction between the two diseases seems to be in the inciting agents, and this can be ascertained only by isolation, identification, and reinoculation with pure cultures of the isolates. *Erwinia dissolvens* (*Phytomonas dissolvens*) has been identified as the inciting organism of the disease. Cells are rod-shaped, nonmotile or motile by a single flagellum, Gram-negative, and $0.5\text{--}0.9 \times 0.7\text{--}1.2 \mu$ in size. Colonies are fast-growing and white. The bacteria penetrate through stomata, hydathodes, or injuries. Hot, humid weather appears optimum for development of this disease.

Another bacterial stalk rot was found by Ark (1940) in California. So far as is known, this is the only record of the disease. The symptoms, which are similar to the disease described above, are recognized by a soft, brown rot of the lower internodes. The bases of leaves at the lower parts of the plant are also attacked. Severely diseased plants fall over. The bacterium isolated from the diseased plants has been named *Phytomonas lapsa*. Cells are rod-shaped, $1.5 \times .56 \mu$ in size, and motile by 1 to 4 polar flagella. The organism was recovered also from beetles (*Diabrotica* sp.), suggesting an insect vector relationship. The bacterium is known to retain its viability on dried seed in the laboratory for over a year (Ark, 1941). Treating the seed with an organic mercury preparation destroyed the organism. Whether this bacterial stalk rot and the one described by Rosen are different diseases may be questioned. Certainly the symptoms of the two diseases and some of the morphological and physiological characteristics of the inciting agents are sufficiently alike to make distinction difficult.

IV. Ear Rots

Corn is susceptible to a number of distinct ear diseases. Five of these are widely distributed and have at times caused appreciable damage. A survey, made by Hoppe (1943), of the relative prevalence and geographic distribution of ear rots over a 10-year period, showed a pronounced interannual variation in the incidence of these diseases and also rather definite areas of occurrence. When these diseases are severe, yield and quality of grain (Stevens and Wood, 1935) as well as nutritive value (Mitchell and Beadles, 1940) are reduced. Infected seed, even though viable, produces weak, unthrifty plants.

1. *Diplodia* Ear Rot

Diplodia ear rot is one of the most prevalent and destructive among the diseases attacking corn ears (Clayton, 1927; Koehler and Holbert, 1930). Durrell (1923) estimated losses from this disease to range from 3 to 15 per cent in Iowa during 1921 and 1922. Boewe (1938) reported the incidence of *diplodia* ear rot to vary from less than 1 per cent to nearly 6 per cent over a 10-year period in Illinois. In a few isolated cases in Indiana the writer has seen up to 15 to 25 per cent of the ears in a given field attacked by this disease.

One of the earliest symptoms of *diplodia* ear rot is the bleaching of husks. Infection may take place from silking until maturity, but ears appear to be most susceptible during the first three weeks after full silk (Raleigh, 1930; Ullstrup, 1949). Infection that occurs at silking time or in the milk stage results in complete rotting of ears and the husks

adhere tightly. Ears are shrunken, lightweight, dull grayish-brown (Fig. 6B). Black pycnidia and grayish-white mycelium of the fungus are evident between the husks and on the undeveloped kernels and cob (Fig. 6A). Ears infected early often remain in an upright position until harvest. Ears infected somewhat later may show fully developed kernels, but white felty mycelium is usually seen between the rows of the grains (Fig. 6C). When infection occurs late in the season ears may show no outward evidence of disease; it is only when they are broken

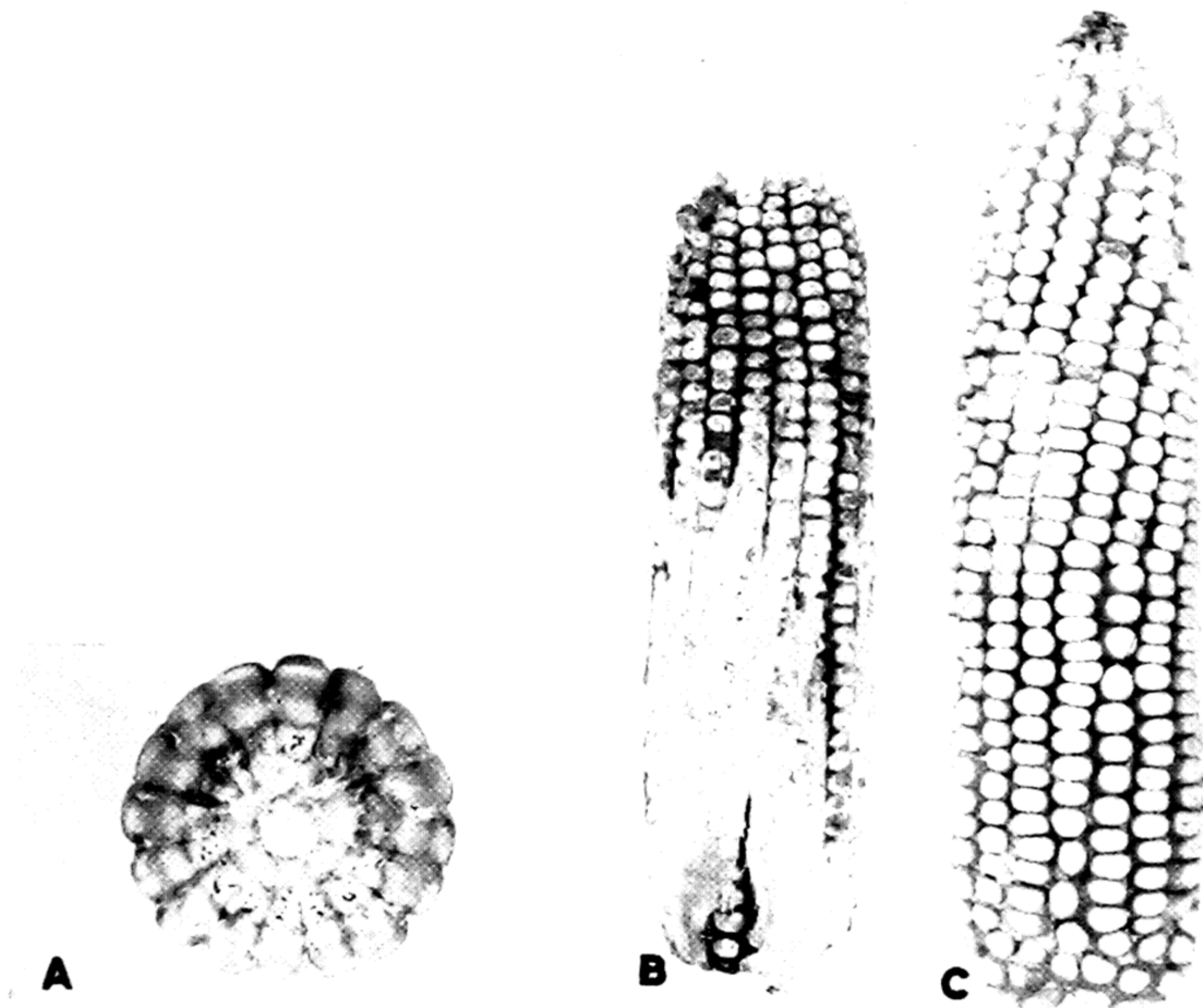


FIG. 6. Diplodia ear rot. A. Cross section of an infected ear showing mycelium and pycnidia. Compare with Figs. 8C and 9A. B. Severely infected ear. Note pycnidia on husks. C. Late infection. Note mycelium between kernels.

or kernels removed that mycelium is seen sparsely developed at the kernel tips and on the cob. Infection takes place usually at the butt end of the ear and progresses toward the tip.

Diplodia zeae is the inciting agent of diplodia ear rot; its morphology and life cycle have been described in the section on diplodia stalk rot. Spores of the fungus are carried by wind to corn ears, where they lodge between the husks or on the silks. When water collects in these places spores germinate and penetrate the ear tissues.

Several factors influence the incidence of diplodia ear rot; among these weather conditions seem to be very important. Heavy rainfall in August and September is especially favorable for the development of

the disease (Durrell, 1923; Koehler, 1950). Husk coverage and the relative declination of the ears appear to have some effect on the incidence of this ear rot. Koehler (1951) has shown that ears with poor husk coverage or those that remain in an upright position for a long time tend to become infected more frequently than do ears that have good husk protection or that show early declination. Koehler pointed out, however, that aside from these morphological characters which affect the incidence of the disease, physiological factors may be equally or more important in determining resistance. Boewe (1936) found poor husk coverage and the incidence of some ear rots to be positively correlated, but concluded that diplodia ear rot and gibberella ear rot may be more frequently associated with good husk coverage. The disparity between these findings may be related to the period when observations were made. If the observations are made in late September and October, after most ear rot infection has been established, many of the diplodia- and gibberella-rotted ears will show tightly adhering husks. Thus good husk coverage and the occurrence of these diseases would be associated. Ears held in an upright position and with loose open husks tend to collect water, thus providing ideal conditions for the germination of spores of *D. zae*. Observations by the writer on a limited number of hybrids suggest that those in which the ears dry rapidly have less diplodia ear rot than do slow-drying hybrids.

The most feasible means of controlling diplodia ear rot appears to be through the development of resistant hybrids. Differences in resistance between inbred lines is marked, but none is immune from infection (Ullstrup, 1949; Koehler, 1953). Although little is known regarding the inheritance of resistance, observations on segregating populations indicate that a number of genes probably determine reaction to this disease. The nature of resistance has not been extensively explored. Johann (1935) made a histological study of the kernels of resistant and susceptible strains of corn, but found no anatomical features associated with the kernels to account for differences in reaction to this ear rot.

2. *Gibberella* Ear Rot

Gibberella ear rot, or red ear rot, occurs over most of the Corn Belt but appears to be somewhat more prevalent in the northern parts of this area. The disease is seldom of major importance; only occasionally in local areas has it been destructive. Corn affected with this disease is toxic to nonruminants.

The distinguishing symptoms of *gibberella* ear rot are the pink-to-red discoloration of the infected ears. When infection takes place early, husks are pink and adhere tightly to the ear. Pink-to-white mycelium

often develops abundantly between the husks. Occasionally the bluish-black perithecia of the fungus are found on the husks and ear shank (Fig. 7A). Infection almost invariably begins at the tip and proceeds toward the butt end of the ear (Fig. 7B).

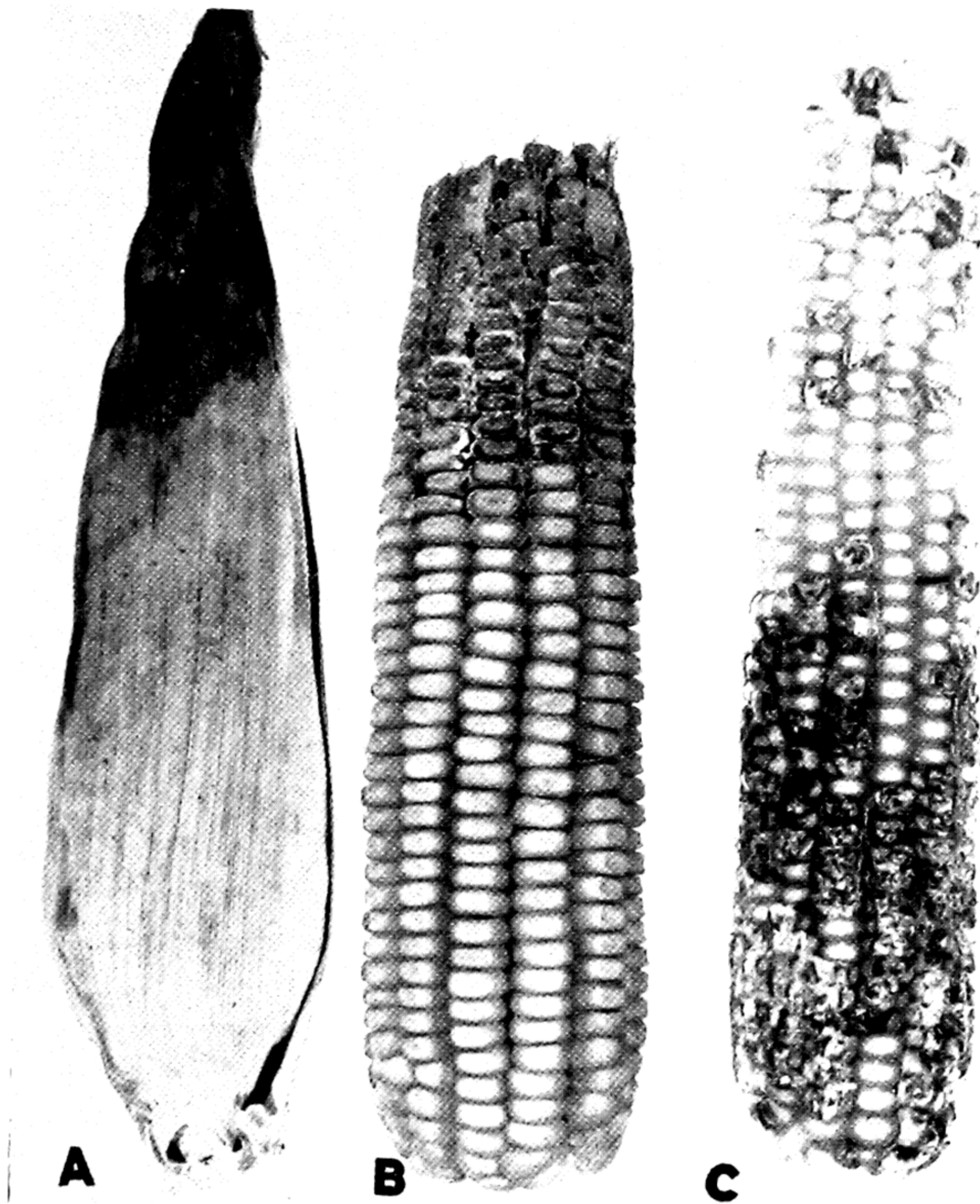


FIG. 7. A. *Gibberella* ear rot. Note tightly adhering husks and black perithecia (immature) developing near tip of the ear. B. *Gibberella* ear rot showing characteristic infection progressing from the tip of the ear. C. *Fusarium* kernel rot. Note random distribution of diseased kernels.

Gibberella ear rot is incited by *Gibberella zeae*. The morphology and life cycle of the fungus have been described under Section III, 2 on *Gibberella* stalk rot.

Cool, wet weather at silking appears to favor development of this ear rot. Hybrids with loose open husks that permit exposure of the ear are more susceptible to the disease than those having good husk coverage.

No control measures have been developed because of the minor importance of the disease.

3. *Fusarium* Kernel Rot

Fusarium kernel rot is widely distributed and can be found to some extent every year. The disease seems to be especially prevalent in the drier parts of the Corn Belt (Hoppe, 1943) and in some of the western states (Smith and Madsen, 1949).

The symptoms of *Fusarium* kernel rot are distinct from those of diplodia and gibberella ear rot in that the infected kernels are usually distributed at random over the ear (Fig. 7C). Infected kernels vary from pale-pink to lavender and often show some cottony wefts of mycelium on their caps. The fungus frequently gains entrance through the channels made by ear worms or corn borers.

The disease is incited by the fungus *Gibberella fujikuroi*. The asexual stage, *Fusarium moniliforme*, has two spore forms. Microconidia, which are most abundant, are hyaline, single-celled, $10.5 \times 4.2 \mu$ in size, and borne in chains or false heads. Macroconidia, which are sparsely produced, are hyaline, 3- to 5-septate, somewhat curved and pointed at the tips, and measure $41.1 \times 4.3 \mu$. Perithecia of the sexual stage, not frequently found in nature, are bluish-black and $275\text{--}380 \times 210\text{--}300 \mu$ in size. Each ascus contains 8 ascospores, which are straight, predominantly 1-septate, and average about $15.3 \times 5 \mu$ in size. A closely related fungus, *G. fujikuroi* var. *subglutinans*, is also frequently associated with pink kernel rot. The morphology of this fungus is similar to that of *G. fujikuroi*, but microconidia are borne always in false heads and never in chains, and the ascospores are shorter and always 1-septate. The perithecia of *G. fujikuroi* var. *subglutinans* occur frequently on old corn stalks. Both fungi overwinter on plant debris.

Factors affecting the prevalence of the disease are not well understood, but on the basis of its geographic distribution it is generally assumed that dry warm weather is favorable. Some inbred lines tend to be more susceptible to *Fusarium* kernel rot than others (Smith and Madsen, 1949). Inbred lines that have a tendency to weak seed coats, which is expressed often as "popped kernels" or "silk cut," are especially susceptible owing to the exposure of endosperm tissue on which the fungus can become established. Ears with poor husk coverage show more *Fusarium* kernel rot than ears with good husk protection.

4. *Nigrospora* Cob Rot

The incidence of *nigrospora* cob rot is variable, but some can be found every year. Although the disease is widely distributed, it is seldom of major importance.

Nigrospora cob rot is ordinarily not conspicuous until the ears are

harvested. The tightly adhering and discolored husks, so characteristic of diplodia, gibberella, and gray ear rot, are not found in this disease. The distinguishing symptom of this rot is the shredding of the cob. This may be found at the tip or butt end of the cob, but the latter site is far more frequent (Fig. 8A). Severely infected ears show a gray discoloration of the internal cob tissues due to the growth of the fungus,

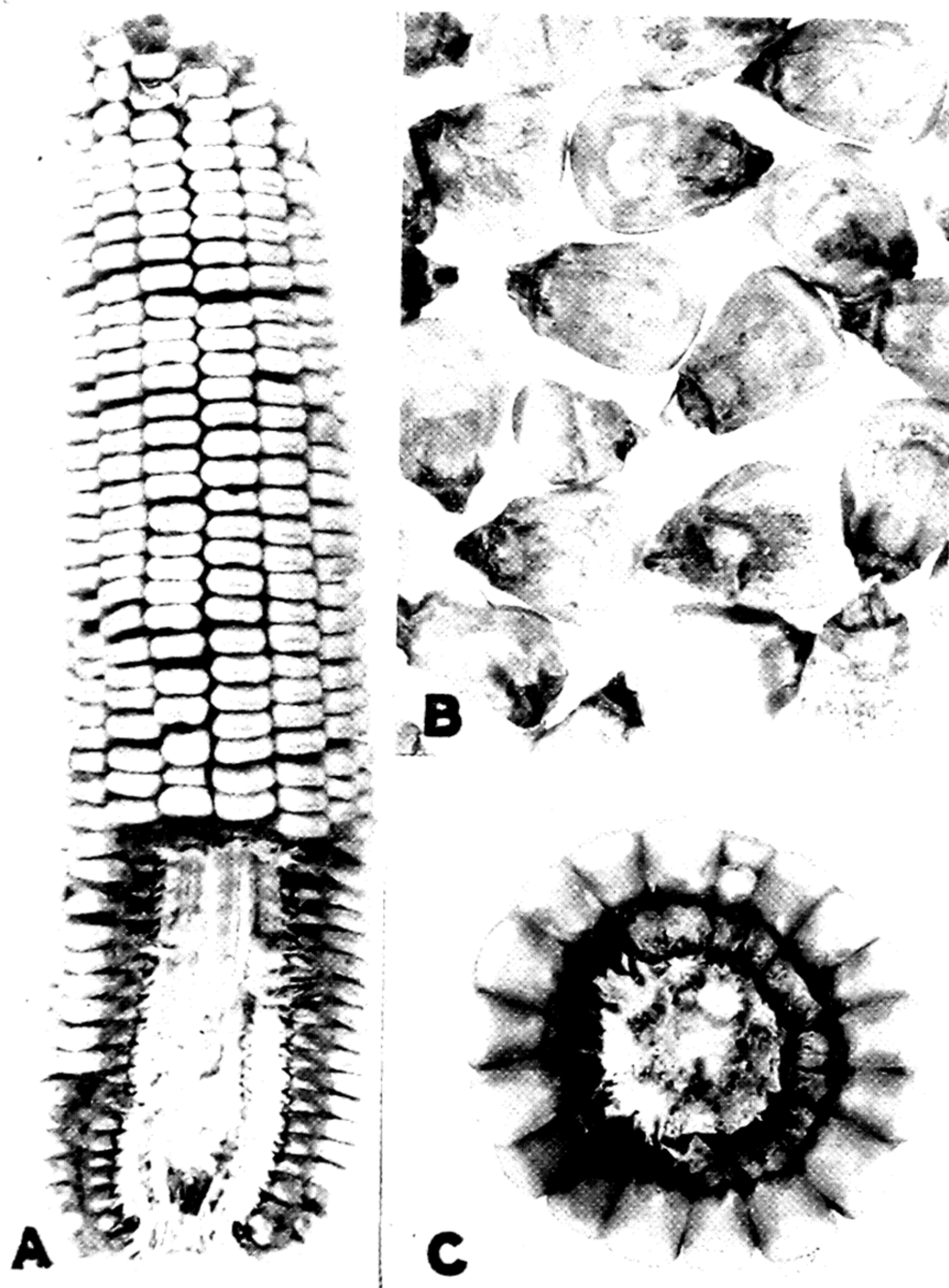


FIG. 8. *Nigrospora* cob rot. A. Infected ear. Note chaffy condition and disintegration of cob. B. Kernels infected with *Nigrospora oryzae* showing black spore masses of the fungus. C. Cross section of an infected ear showing black spore masses on the chaff.

and the pith may be completely disintegrated, leaving only the vascular bundles intact. Kernels often show the development of masses of minute black spores of the pathogen near their tips (Fig. 8B, C). Ears are lightweight, and kernels are bleached and loose on the cob.

Nigrospora oryzae (*Basisporium gallarum*) is the inciting agent of this disease. Spores of the fungus are black, oval to spherical in shape,

10 to 20 μ in diameter, and are borne on short branches of the mycelium. No sexual stage of the fungus is known. The fungus overwinters on infected corn tissue and particularly on undeveloped secondary ears (Standen, 1939).

This fungus is not an aggressive parasite and attacks ears only after plants have been weakened or injured by frost, drought, or stalk rot before fully mature (Durrell, 1925). When heavy rainfall follows any condition that weakens the plants, the incidence of the disease increases (Durrell, 1925).

Reddy (1933) and later Standen (1944, 1945) studied the nature of resistance to nigrospora cob rot and concluded that low pH of cob tissue and resistance to infection were positively correlated. Immature cob tissue was found to have a higher pH and to be more susceptible than fully matured cob tissue. In addition to the relation between pH and susceptibility, Standen (1944) found that immature cobs contained a substance or substances, presumably organic, that favored growth of the fungus. This nutritive material was not identified, but it was more abundant in poorly matured cobs than in well-matured cobs.

No specific control for nigrospora cob rot has been devised. The fact that the fungus is a weak parasite and attacks ears on plants which have been weakened or killed before reaching maturity, suggests that the use of full-season and adapted hybrids may be the most practical means of avoiding losses from the disease.

5. Gray Ear Rot

Gray ear rot occurs over most of the eastern half of the United States, but it is not of major importance. In isolated cases the incidence of the disease has reached as high as 10 per cent (Ullstrup, 1946).

The first symptoms of the disease resemble those of diplodia ear rot, and the two diseases are easily confused (Fig. 9C). White, felty mycelium is frequently seen between the husks and embedded between the kernels. Ears infected early remain in an upright position; husks adhere tightly and become slate-gray in color (Fig. 9B). The cob and kernels are completely permeated by the gray-to-black mycelium of the fungus. When infected ears are broken, minute black sclerotia are found scattered through the tissues. Infected kernels may show black striations or sclerotia beneath the pericarp (Fig. 9D). The presence of sclerotia and the dark-gray color of the ear in advanced stages of infection distinguish this disease from diplodia ear rot (Fig. 9A).

The fungus inciting gray ear rot is *Physalospora zeae*. The asexual stage, *Macrophoma zeae*, was described first by Tehon and Daniels (1927). They found the fungus in large lesions on corn leaves. Pycnidia

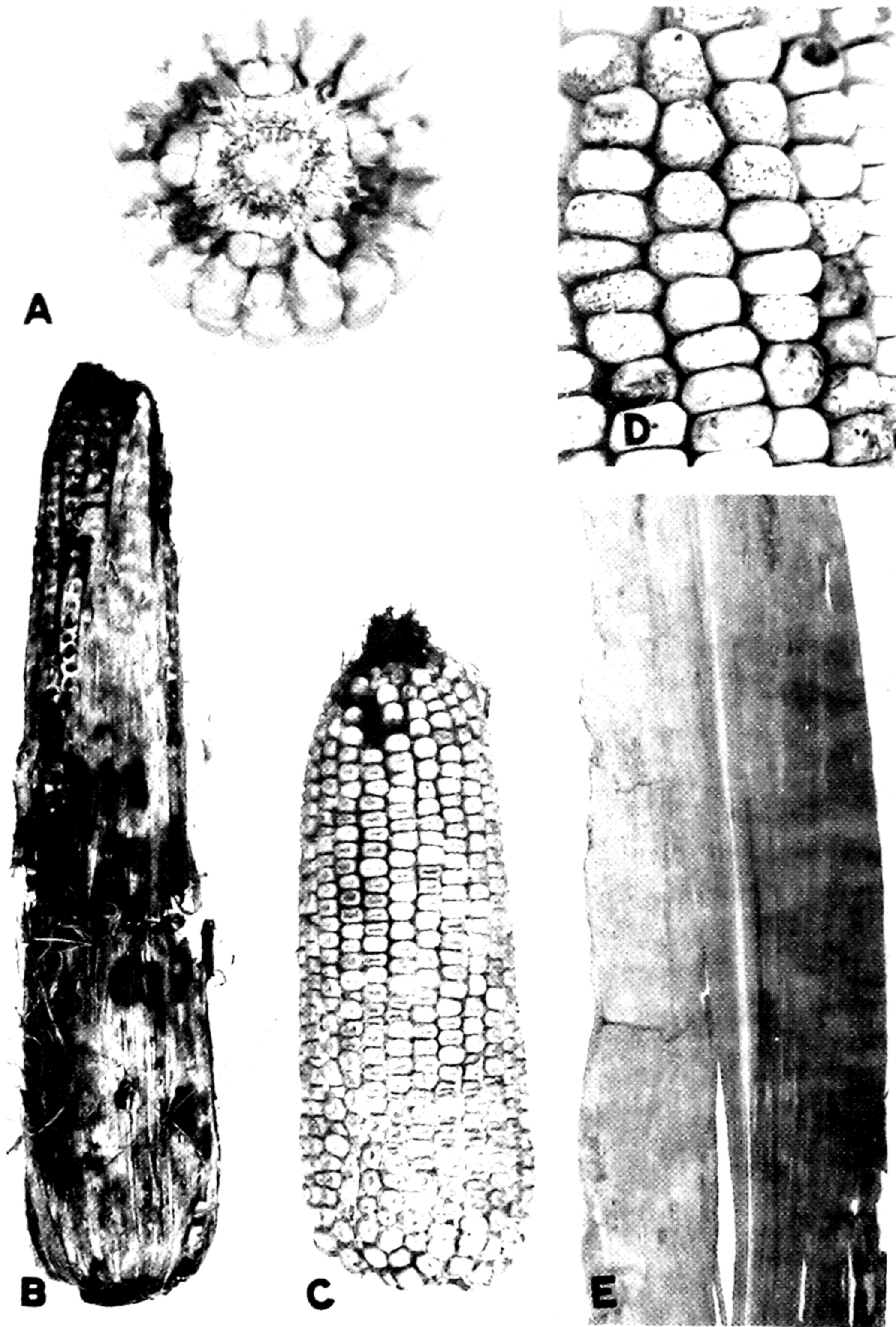


FIG. 9. Gray ear rot. *A*. Cross section of an infected ear showing typical appearance of the cob with the development of small black sclerotia in the pith. *B*. Severely rotted ear. *C*. Mildly infected ear resembling diplodia ear rot (Fig. 6*C*). *D*. Sclerotia beneath pericarp of kernels. *E*. Perithecia and pycnidia of *Physalospora zeae* in a leaf lesion (minute specks on left side of leaf).

are round to oval, black, carbonous, embedded in the mesophyll, 65 to 120 μ in diameter, and provided with ostioles which protrude through the upper surface of the leaf. Spores are hyaline to pale-greenish, single-celled, oval to fusiform, and $17-31 \times 6.5-8.5 \mu$ in size. The sexual stage of the fungus was described first by Stout (1930), who found perithecia

in leaf lesions along with the pycnidia of the asexual stage. The relationship of the fruiting structures was suspected but not proved. Perithecia are embedded in the mesophyll, opening by minute papillate ostioles to the upper surface of the leaf, black, carbonous, globose, and 75–235 μ in diameter. Asci are stalked, straight to curved, double-walled, 85–150 $\times$ 13–22 μ , and contain 8 ascospores. Paraphyses are obscure, hyaline, and filamentous. Ascospores are hyaline to dilute olivaceous, one-celled, ellipsoid, 19–25 $\times$ 6.5–8 μ in size. A third type of fruiting body has sometimes been observed. These are small, black, flask-shaped structures with one or two long, tapering beaks, and contain minute, single-celled, hyaline spores. These spores are exuded in a viscous matrix from ostioles at the apices of the long beaks. Germination of the spores has not been observed, and their function, if any, is unknown. The leaf lesions, in which the fruiting structures of both the asexual and sexual stages are found, are tan to grayish-brown and dry and brittle, ranging in size from 1 $\times$ 2 inches to 4 $\times$ 18 inches (Fig. 9E). Pycnidia and perithecia develop also on stalks immediately below the tassel. Fruiting bodies of the fungus have never been observed on the ears. The relationship between *P. zeae* and *M. zeae*, the sexual and asexual stages of the organism, and proof of pathogenicity of the fungus on corn ears has been established (Ullstrup, 1946). Spores of the fungus overwinter in the leaf lesions and in the following year are carried by wind to ears and leaves, where they germinate and initiate infection.

The factors influencing the prevalence of the disease are not fully known, but judging from the geographical distribution of the organism, warm humid weather in August and September appears to be favorable for infection.

Knowledge concerning the reaction of inbred lines or hybrids to the disease is insufficient to warrant recommendations for control on the basis of relative resistance. Cultural practices or soil fertility do not appear to influence the prevalence or severity of gray ear rot.

6. Other Ear Rots

Physalospora ear rot was described first by Eddins (1930b). The disease is not important and seems to be confined to the Gulf Coast states. The disease when fully developed is recognized by a dark-brown, felty mycelial growth on all parts of the ears. The interior of severely infected tissue is blackened and completely overrun by the fungus. Mildly infected ears show only a few blackened kernels. Infection is initiated generally at the butt of the ear. *Physalospora zeicola* is the inciting agent of the disease. Pycnidia of the asexual stage, *Diplodia frumenti*, are globose, black, 170 to 470 μ in diameter, and emerge in

masses through longitudinal cracks on the exterior of corn stalks. Pycnospores are 1 septate, oval, striated, light- to dark-brown, and $20\text{--}28 \times 11\text{--}15 \mu$ in size. *D. frumenti* is distinguished from *Macrophoma zae* on the basis of the size, shape, color, and number of septations of the pycnospores. Pycnidia of the former develop in pure culture on agar substrates; those of the latter have never been found to do so. The sexual stage, *P. zeicola*, was described first by Ellis and Everhart (1890). Asci are double-walled, contain 8 ascospores, and are $95\text{--}140 \times 10\text{--}13 \mu$ in size. Ascospores are hyaline, granular, unicellular, oval, and $20\text{--}23 \times 8\text{--}9 \mu$ in size. *P. zeicola* is distinguished from *P. zae* by its shorter asci and shorter and broader ascospores. Fruiting structures of both the sexual and asexual stages of the fungus are found on old corn stalks and husks. The relation between the two stages of the fungus was pointed out by Eddins and Voorhees (1933). No information is available on the reaction of inbred lines or hybrids that might be used as a basis for control of the disease.

Rhizoctonia ear rot occurs in Florida and some of the other Gulf Coast states. In early stages of infection husks and kernels are covered with a salmon-pink mycelial growth of the fungus. As the disease progresses, the color of infected parts becomes dull-gray, and white-to-dark-brown sclerotia of the fungus develop on the outer husks. The disease is incited by *Rhizoctonia zae* (Voorhees, 1934). No spores are known to occur in the life history of the fungus. The organism is carried over from one season to another as dormant mycelium and sclerotia in the seed, in the soil, or on plant debris. The distribution of the disease and the relatively high optimum temperature for growth of the fungus ($33^{\circ}\text{C}.$) suggests that warm humid weather is conducive to infection.

Southern diplodia ear rot is found in the southeastern part of the United States. The symptoms of the ear rot are very similar to those of diplodia ear rot described above. *Diplodia macrospora* is the inciting fungus and resembles *D. zae* in most respects except that the spores are much larger ($68 \times 9 \mu$). The fungus attacks stalks and leaves as well as ears. The disease has been fully described by Eddins (1930a).

A number of other fungi may cause ear and kernel rots. *Penicillium* ear rot is recognized by the characteristic greenish-blue fluffy mold growing on and between the kernels. "Blue eye," a storage rot incited by certain species of *Penicillium*, appears as a blue-green discoloration of the germ. Ear and kernel rots incited by species of *Aspergillus* are identified by black or green, powdery masses of spores. Hormodendrum kernel rot is seen as a greenish-black mold on the caps of the kernels. All of these fungi are widely distributed and are generally saprophytic in nature. Very frequently they gain access to ears through injuries

caused by ear worms or corn borers. These ear and kernel rots sometimes become prevalent when warm, humid weather prevails after ears are mature. These fungi frequently continue to develop in stored corn when the moisture content of the grain is high.

V. Leaf Diseases

The importance of some leaf diseases, namely, northern corn leaf blight, southern corn leaf blight, and bacterial wilt, has increased during the past 15 years. Within this period several epiphytotics of one or another of these diseases have occurred. The severity of leaf diseases is variable, and a given set of environmental conditions favoring one of these diseases is not necessarily optimum for the development of another. Severe development of leaf diseases not only reduces grain yield but also increases the susceptibility of plants to stalk rots.

1. *Northern Corn Leaf Blight*

Northern corn leaf blight is found in most of the humid areas where corn is grown. In the United States it occurs most frequently from the eastern half of the Corn Belt to the Atlantic coast and southward. Localized epiphytotics have occurred outside this general area in some years.

The epiphytology of this leaf blight is not fully known. Observations suggest that the disease is favored by comparatively moderate temperatures and heavy dews during the growing season. Following a season in which little or none of this leaf blight is present, there is a gradual increase in prevalence in subsequent years. In 1943 the disease was widespread in southeastern Indiana and southern Ohio; in 1944 the incidence of northern corn leaf blight was negligible because of dry hot weather. In the years following the disease increased gradually until the peak year of 1951, when it could be found over much of the eastern part of the Corn Belt. In the comparatively hot dry growing season of 1952 very little of this leaf blight could be found through Illinois, Indiana, and Ohio, but it was relatively abundant in Wisconsin, where temperatures were more moderate. In any growing season when the disease is prevalent a gradual increase in severity is generally observed as the season progresses. This is probably due largely to successive infections, but there is some evidence also that susceptibility in corn increases with age of the plants. Inoculum may overwinter in infected corn leaves as dormant mycelium on which spores are produced the following growing season (Robert and Findley, 1952). The occurrence of the disease in isolated locations suggests that inoculum may be wind-borne and deposited as "spore showers."

Reduction in grain yield due to northern corn leaf blight depends on the severity and earliness of establishment of an epiphytotic. In an artificially induced epiphytotic yield reductions of 40 to 68 per cent were found in very susceptible hybrids (Ullstrup, 1951). Resistant hybrids showed nonsignificant yield losses. In this experiment the disease was severe on the susceptible hybrids by August 10, or about two weeks after full silk. In later studies in which the disease did not become severe on susceptible material until September 15 or about six weeks after silking, no significant losses in yield were evident even in very susceptible hybrids.

The symptoms of northern corn leaf blight appear as long, elliptical grayish green or tan spots ranging up to 6×1.5 inches in size (Fig. 10A). The time required for distinct lesions to appear after inoculation is usually about 7 to 10 days. Lesions develop first on the lower leaves, and as the season progresses their numbers may increase until all leaves are nearly covered with them and little green tissue remains. Spores of the pathogen are produced on the lesions in damp weather. Often these spores are arranged in concentric zones so that a target-like design is evident. Observations made under both artificial and natural epiphytotics indicate that kernels are not attacked; thus the possibility of seed transmission of this disease is very remote.

Helminthosporium turcicum is the name of the fungus inciting northern corn leaf blight. The fungus and the disease were first described by Passerini in Italy in 1876. Spores germinate and penetrate corn leaves within a few hours in the presence of free water and when the temperature range is 75° to 85°F . Spores are olive-gray, spindle-shaped, often curved on one side, average $105 \times 20 \mu$ in size, and have 1 to 9 septations (Fig. 10B). A conspicuous and identifying feature of the spores is the protruding hilum. No sexual stage of the fungus is known.

Helminthosporium turcicum attacks corn, Sudan grass, and sorghum. In preliminary experiments Lefebvre and Sherwin (1945) found that isolates from Sudan grass, Atlas sorghum, Johnson grass, and corn differed in their ability to infect host testers employed. Two cultures from Sudan grass and one from Atlas sorghum were pathogenic on Gooseneck sorghum and Sudan grass, but all failed to infect corn. Four isolates from corn infected Sudan grass and two did not. All six cultures from corn were pathogenic on corn. Isolates from Johnson grass were pathogenic only on Johnson grass. The existence of pathogenic races within the species may explain why corn growing near heavily infected Sudan grass is sometimes free of the disease. So far as is known at present isolates of the fungus from corn have not shown

any indication of specialization in parasitism on inbred lines of corn. Robert (1952) observed variation in cultural behavior and pathogenicity of *H. turcicum*.

Inbred lines differ strikingly in their resistance to this leaf blight, but only very few are highly resistant (Elliott and Jenkins, 1946).

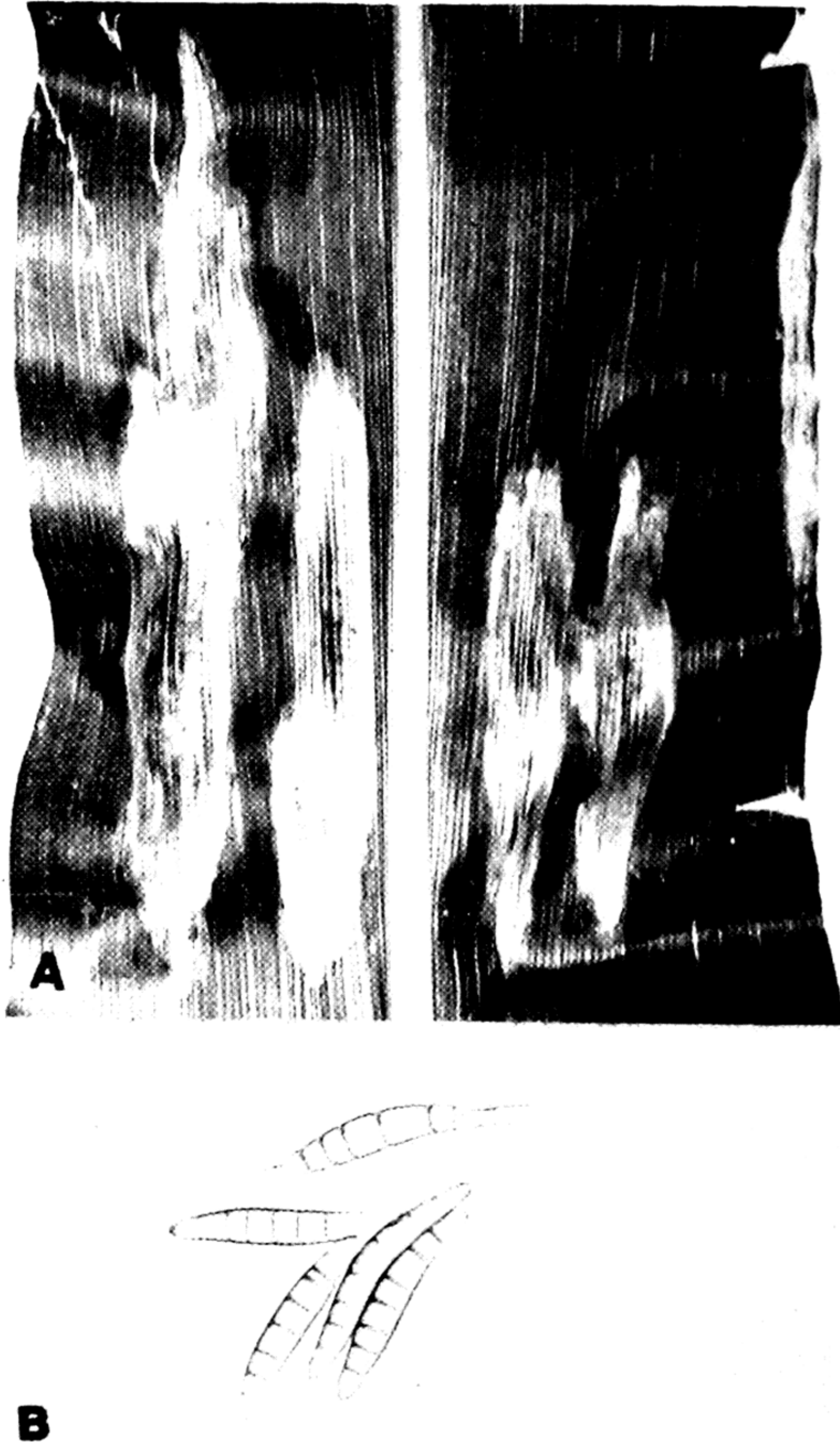


FIG. 10. Northern corn leaf blight. *A.* Typical elliptical lesions of the disease. *B.* Spores of *Helminthosporium turcicum*, the inciting agent of northern corn leaf blight.

Most of the well-known inbred lines used in the Corn Belt are very susceptible. Among the best sources of resistance which have proved suitable as parental material in breeding programs are Mo21A, NC34, L97, and Ky114. Yellow inbred lines somewhat less resistant than the white inbreds listed above are Ky36-11, K148, K175, K201, K230, R39, and C103. Studies by Jenkins and Robert (1952) and by Jenkins *et al.* (1952) indicate that resistance is determined by many genes. They sug-

gest that same inbred lines carry major genetic factors for resistance and others may contribute minor genes of lesser effect. None of the highly resistant lines is immune from infection; all will show a few restricted lesions under severe disease development. Resistance is not expressed until plants are several weeks old. The progress that has been made in breeding for resistance offers promise of eventual control of the disease through the use of resistant hybrids.

The only other known means of controlling northern corn leaf blight is by spraying or dusting plants with fungicides. This method has been used successfully on sweet corn in Florida (Stoner, 1950, 1951; Townsend, 1951). The fungicides most effective were Dry Parzate, SR-406, and Dithane Z-78. Eleven applications were necessary for the best control.

2. Southern Corn Leaf Blight

Southern corn leaf blight occurs on corn in many warm humid areas of the world. In this country it is found chiefly in the southeastern states, but its range may, in some seasons, extend into southern parts of the Corn Belt and eastward to the Atlantic seaboard. The disease appears to thrive under conditions of high humidity and somewhat higher temperatures than northern corn leaf blight.

The symptoms of this disease are distinct from those of northern corn leaf blight. Lesions are much smaller, ranging up to $1-2 \times 0.25-0.5$ inches in size and distinguished by their tendency to have parallel sides (Fig. 11A). This characteristic shape appears to be due to the limitation of lateral spread of the fungus in the tissue by the vascular bundles of the leaf. The width of lesions may be modified to some extent depending on the host; on some inbred lines they are much narrower than on others. The lesions are tan or straw-colored and on some inbred lines may show a faint purplish margin. The disease is seldom, if ever, found on the grain; therefore seed transmission seems unlikely.

The fungus inciting southern corn leaf blight, *Cochliobolus heterostrophus*, was first described by Drechsler (1925) under the binomial *Ophiobolus heterostrophus*. He found the fungus on corn leaves collected in Florida and in the Philippine Islands. The asexual stage was described in Japan by Nisikado and Miyake (1926), who assigned it the name *Helminthosporium maydis*. Later Drechsler (1934b) changed the name of the fungus from *O. heterostrophus* to *C. heterostrophus*. Conidia range in color from pale-smoky to olive-brown, have 3 to 13 septations, average $90 \times 15 \mu$ in size, and show greater curvature than conidia of other species of *Helminthosporium* parasitizing corn (Fig. 11B). Perithecia are black, 0.4 to 0.6 mm. in diameter, and beaked.

Asci measure $160\text{--}180 \times 24\text{--}28 \mu$ and contain up to 8, but typically 4, ascospores. Ascospores are pale, smoky-colored, $130\text{--}340 \times 6\text{--}7 \mu$ in size, bear 5 to 9 cross walls, and are in a helicoid arrangement within asci. The sexual stage is not abundant in nature, and its role in the



FIG. 11. Southern corn leaf blight. A. Leaf lesions. B. Spores of *Helminthosporium maydis*.

propagation of the fungus may be unimportant. This sparsity of the sexual stage in comparison with the occurrence of the asexual stage may account for the reason why the name under which the latter was first described, *H. maydis*, has attained common usage among plant pathologists in this country. No specialized pathogenic races are known to exist within the species. The fungus will also attack teosinte.

Southern corn leaf blight does not appear to reduce grain yields so much as northern corn leaf blight. In a limited number of experiments the author found 20 to 30 per cent yield reductions in very susceptible hybrids under severe artificially induced epiphytotics. Yield losses under natural conditions are probably much less than these figures.

Inbred lines differ strikingly in resistance to this disease. Yellow inbred lines of exceptionally high resistance are CIO3, Tr, MoG, W20, and Os426. The white inbred lines Ind 33-16, Ky27, and K64 are also resistant. Resistance is not apparent in the young seedling but is rather clearly defined in plants several weeks old. Pate (1950) concluded from preliminary studies that resistance is probably determined by several genes. Control of the disease will be accomplished ultimately through the development of resistant hybrids.

3. *Helminthosporium Leaf Spot*

This disease was observed first in Indiana in 1938. Since that time it has been found in many states from Iowa eastward to the coast. The disease thrives under moderate temperatures and high relative humidity.

Lesions produced following infection by race I of the fungus are recognized as tan, oval spots ranging up to 1×0.5 inch in size (Fig. 12A). A zonate pattern is fairly distinct in the lesions. All parts of susceptible plants are attacked. In damp weather spores are produced in profusion, especially on leaf sheaths. Unlike the two leaf blights described above, this disease attacks the ears, imparting a black charred appearance to them (Fig. 13B). For this reason the disease can be disseminated by infected seed. Symptoms incited on leaves by race II appear as narrow chocolate brown spots 1×0.25 inch in size. Leaf symptoms incited on seedlings by this race are recognized as long, narrow, tan spots of irregular shape.

Helminthosporium carbonum is the fungus inciting the disease. The species appears to be composed of two races which are separable on the basis of virulence, specialization in parasitism to certain inbred lines, and symptoms incited on corn leaves. The races are alike in morphology, cultural characters, and symptoms they incite on ears (Ullstrup, 1944). Spores are spindle-shaped, slightly curved, and $25\text{--}100 \times 7\text{--}18 \mu$ in size, with mean measurements of about $62 \times 13 \mu$ (Fig. 12B). The number of cross walls varies from 2 to 12, with an average of about 6. Spores are olivaceous-brown and distinctly darker than those of *H. turcicum* or *H. maydis*. No sexual stage of this fungus is known, and corn is the only host. Race I is highly virulent on suscep-

tible inbred lines. Race II is only mildly virulent, and the disease incited by it is never of economic importance.

Resistance to race I is general; only a few inbred lines are susceptible. Among the known susceptible inbreds are Mo21A, Pr, K61, and



FIG. 12. *Helminthosporium* leaf spot. *A*. Typical leaf lesions on a susceptible inbred line. *B*. Spores of *Helminthosporium carbonum*. Note that these spores are darker and somewhat straighter than those of the other two species.

K44. Susceptibility and resistance to infection by race I are sharply differentiated. Resistant inbred lines show only minute necrotic flecks where the pathogen has penetrated, whereas susceptible inbred lines exhibit typical, well-defined lesions five to seven days following inoculation (Fig. 13A). Resistance to race I is determined by a single domi-

nant gene located on chromosome 1 (Ullstrup and Brunson, 1947). Because of the complete dominance of resistance the disease is of very little economic consequence. Plant breeders and those maintaining foundation seed stocks have sometimes experienced difficulty in propagating susceptible inbred lines. Inheritance of resistance to infection by race II has not been studied, but it is probably determined by a number

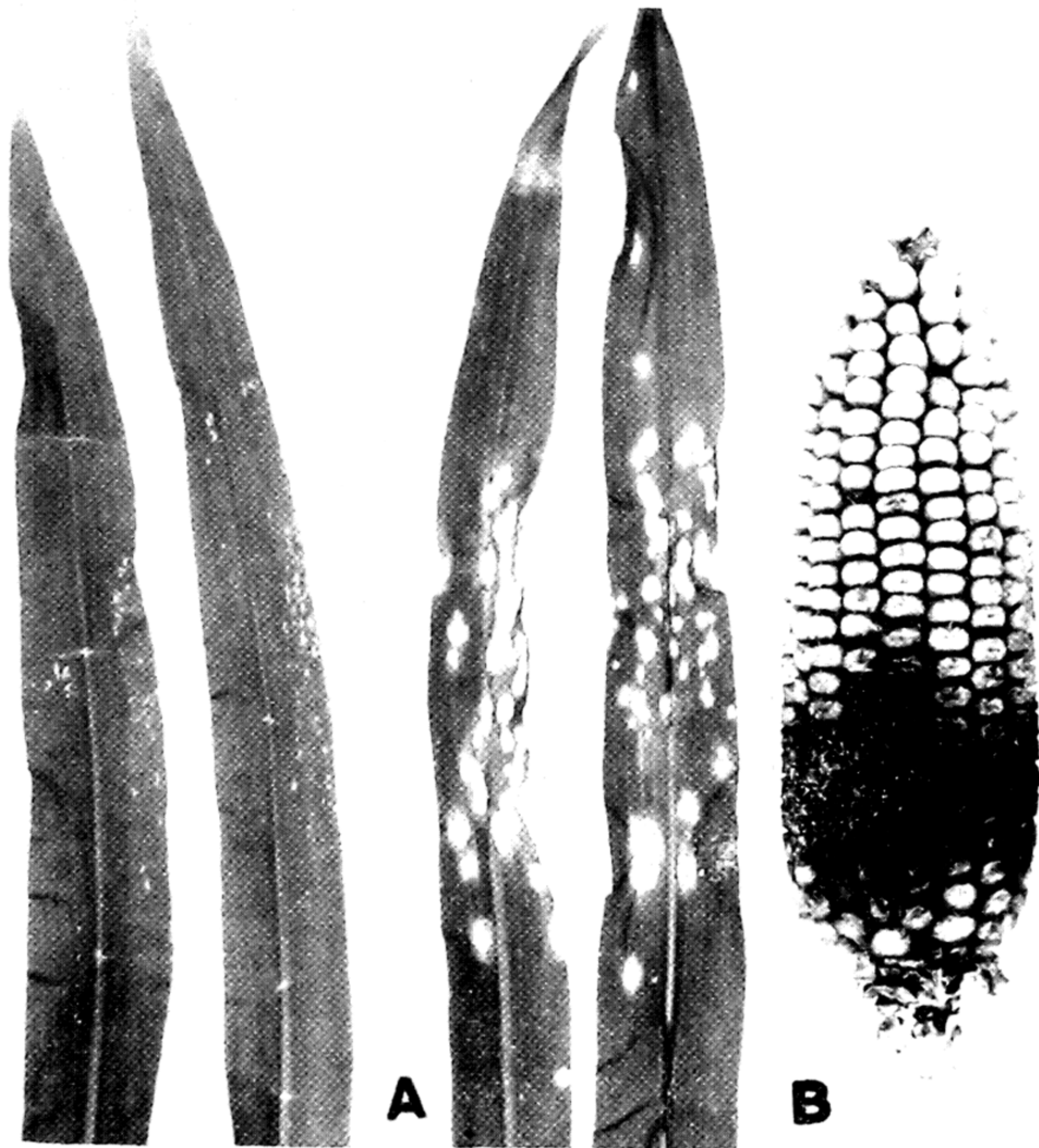


FIG. 13. *Helminthosporium* leaf spot. *A. Left:* Two seedling leaves of a resistant inbred line showing the characteristic flecking following inoculation by *H. carbonum* Race I. *Right:* Two seedling leaves of a susceptible inbred line with typical lesions following inoculation with the same race. *B.* Ear rot incited by *H. carbonum*. Symptoms incited on ears by Race I and by Race II are indistinguishable.

of genes. Differences between inbred lines in reaction to infection by race II are not nearly so clear-cut as found in the case of race I.

4. Bacterial Wilt

This disease, variously known as bacterial wilt, Stewart's wilt, Stewart's disease, or Stewart's leaf blight, was described first in the United States by Stewart (1897). It is most frequently found in the northeastern part of this country from Iowa eastward to the Atlantic coast. The disease is known to occur also in Europe, Africa, Puerto Rico, Mexico, and Canada.

Unlike the leaf blights described above, bacterial wilt does not require damp weather and heavy dews for rapid spread and development. Conditions accentuating rapid transpiration such as hot dry weather, low relative humidity, and rapid air movement increase the severity of symptoms in infected plants. Winter temperatures appear to have a marked influence on the incidence of this disease. It has been pointed out that in summers following mild winters the prevalence of bacterial wilt is generally higher than in growing seasons preceded by severe winters (Stevens, 1934; Haenseler, 1937; Stevens and Haenseler, 1941). Where the sum of the mean temperatures for December, January, and February in degrees Fahrenheit is 100 or more, bacterial wilt may be expected to be severe on susceptible corn during the following summer; whereas if this sum is 90 or less, little, if any, of the disease is likely to be present. This relationship between winter temperatures and the occurrence of bacterial wilt has been used as the basis for predicting the prevalence of the disease (Stevens, 1936; Stevens and Haenseler, 1940). These forecasts have proved to be fairly accurate. For example, Boewe (1953) predicted a severe outbreak of the disease in Illinois on the basis of temperatures during the winter of 1952-53. In the summer of 1953 the prevalence of bacterial wilt was the greatest in recent years.

The effect of winter temperatures is not on the inciting agent of the disease directly, but rather on its insect vector. Rand and Cash (1924) found that bacterial wilt could be transmitted from diseased to healthy corn plants by the corn flea beetle, *Chaetocnema pulicaria*, the toothed flea beetle, *C. denticulata*, and the spotted cucumber beetle, *Diabrotica undecimpunctata*. Poos and Elliott (1936) and Elliott and Poos (1940) have confirmed this work and in addition demonstrated that the bacterium inciting bacterial wilt was carried over winter in the bodies of these insects. Ivanoff (1933) reported transmission of the disease by larvae of *Diabrotica longicornis* and *Phyllophaga* sp. during the course of their feeding on corn roots in infested soil. Poos and Elliott (1936) consider transmission of the disease from soil to healthy plants to be exceedingly rare. Of the many insects studied as possible vectors, Elliott and Poos (1940) concluded that *C. pulicaria* was, by far, the most important in this respect. The survival of this insect has been shown to be favored by mild winter temperatures (Elliott and Poos, 1940). Successful overwintering of large numbers of infested flea beetles increases proportionately the chances of transmission of the disease the following summer.

The host range of the bacterium inciting bacterial wilt is relatively restricted. Ivanoff (1935) was able to induce symptoms of the disease, following artificial inoculation, in sorghum, Sudan grass, yellow fox-

tail, German foxtail millet, and common millet. Elliott and Poos (1940) tested the reaction to this disease of a large number of grasses subjected to both natural and artificial inoculation. Species and varieties of *Coix* and *Euchlaena* were fully susceptible and capable of functioning as



FIG. 14. Stewart's wilt on sweet corn. Note stunting, streaking, and wilting.

natural hosts for the bacterium. Observations suggest that in the United States hosts other than corn probably are not important in the epiphytology of the disease.

Symptoms of bacterial wilt on sweet corn leaves appear as long, irregular pale-green or yellowish streaks which become progressively necrotic. Severely infected plants are stunted, wilt rapidly (Fig. 14),

and often show cavities in the pith. When stalks of such plants are cut, yellowish masses of bacteria ooze from the severed ends of the vascular bundles. Plants which are not killed remain stunted, tassel prematurely, and are frequently barren. Infection may spread throughout the vascular system and pass through the cob into the kernels. Infected kernels are shriveled and darker in color than healthy seeds, and may serve as a means of disseminating the disease.

On dent corn the disease is generally less severe, although certain inbred lines may be fully as susceptible as some sweet corn inbreds and hybrids. Lesions on leaves of dent corn resemble those on sweet corn except that they are somewhat more restricted and originate at points where flea beetles have fed (Fig. 15A, B). Wilting and death are not typical manifestations of the disease in dent corn. The leaf streaking on dent corn frequently is called Stewart's leaf blight, or late infection phase, as distinguished from the fully systemic development of the disease occurring in sweet corn. The late infection phase, as the name implies, becomes increasingly more severe after silking. In very susceptible material extensive leaf killing may occur.

Bacterial wilt is incited by a species of bacteria known as *Bacterium stewarti*. The organism has also been referred to as *Phytomonas stewarti*, *Pseudomonas stewarti*, and *Aplanobacter stewarti*. The binomial cited above, *B. stewarti*, is presently accepted as correct. The cells are short, nonmotile, non-spore-forming, Gram-negative rods, and range up to $2 \times 0.7 \mu$ in size. Colonies on nutrient dextrose agar are small, slow-growing, and pale yellow. The bacterium has been shown to be variable in cultural behavior and pathogenicity. Holbert *et al.* (1933) reported the isolation of atypical strains of the organism from infected plants. By means of continued subculturing and single colony selection, McNew (1937b) isolated from pure cultures, strains of the organism which differed widely in virulence. Ivanoff *et al.* (1938) studied the variability of *B. stewarti* and were able to group isolates of the organism into three broad classes based on cultural behavior, physiological characters, and pathogenicity. Their work indicated that certain of these classes of cultures predominated in some localities during given seasons. McNew (1938) found that high virulence was correlated always with the ability of such cultures to use inorganic sources of nitrogen. Most virulent cultures were able to reduce nitrates to nitrites, but nitrites were found not to be the sole cause of wilting in the host plant. Slightly virulent forms could not use inorganic nitrogen. Successive passage of the organism through resistant inbred lines of corn has been shown to increase the virulence of the initial culture for corn (Wellhausen, 1937a). In contrast, serial passage through susceptible inbred lines de-

creased virulence for corn. Virulence could not be increased beyond a certain point in resistant corn nor reduced beyond a certain point in susceptible corn. The parasite appeared to reach a stage of equilibrium with the host and the environment after which further serial passage



FIG. 15. Stewart's leaf blight on dent corn. *A*. Leaves of dent corn showing decreasing severity of the disease from left to right. *B*. Early development of infection centering around the feeding injuries of the corn flea beetle. Note that infection did not develop around a few of the points of feeding.

had no effect. Serial passage through a susceptible selection of teosinte decreased virulence for both teosinte and corn. Successive passage through highly resistant grass hosts, unrelated to corn, decreased virulence for corn but increased virulence for the specific hosts through which they were passed. Cultures highly virulent for corn produced

slimy growth on nutrient dextrose agar; weakly virulent cultures produced firm growth on this medium. Lincoln (1940) verified this work of Wellhausen with respect to changes in virulence following serial passage of the organism through inbred lines of corn which differed in resistance. He noted also the same correlation between the consistency of growth of cultures and their virulence. Lincoln inoculated resistant and susceptible inbred lines with mixtures of known portions of virulent and avirulent strains, and at suitable intervals assayed the direction and rate of change in proportion of the two types. He concluded that direction and intensity of selection for virulence change are dependent largely on the resistance or susceptibility of the host. Mutation rates were calculated for colony morphology and colony color, and were found to range from 1 in 20,000 to 1 in 800,000 single cells. Mutants were found that were more virulent than the parent cultures; others were less so. Mutation and natural selection within the host were shown to be important agencies in bringing about changes in virulence during host passage. Whereas marked variations in pathogenicity have been demonstrated in *B. stewarti*, none of these studies has indicated the existence of differential pathogenicity. Highly virulent cultures have been relatively highly virulent on all inbred lines tested, whereas slightly virulent cultures have shown relatively low virulence on all inbred lines.

Wide differences exist in resistance to bacterial wilt. In general dent corn is more resistant, popcorn somewhat less so, and sweet and flint corn most susceptible. Since considerable variation in resistance is evident among inbred lines within these broad classes, there is overlapping in this respect between classes. In a study of the reaction of open-pollinated varieties of dent, sweet, and flint corn to this disease, Ivanoff (1936) found a high positive correlation between resistance and plant height, and between resistance and lateness within each group. A few dent corn varieties of certain height and lateness were no more resistant than sweet and flint corn varieties of comparable height and lateness. Ivanoff and Riker (1936) observed these same general positive correlations in sweet corn inbreds and hybrids following inoculation with *B. stewarti*. As in the previous study a few deviations were noted wherein short, early inbreds were resistant and tall, late inbred lines tended to be susceptible. Dominance of resistance was observed generally among the single-cross hybrids involving both resistant and susceptible parents.

In a study of the inheritance of resistance to bacterial wilt, Wellhausen (1937b) verified the general tendency of resistance to be dominant. A few single crosses between inbred lines of intermediate resist-

ance were more resistant than either parent. An analysis of F_2 , F_3 , and backcross progenies indicated two major and one minor, dominant, supplementary, and independently inherited genes, operative in determining resistance to bacterial wilt in corn. Wellhausen observed an association between red cob color and resistance and between white cob color and susceptibility, suggesting some degree of linkage between the gene for cob color and the genes governing resistance to the disease. Lateness and resistance, and earliness and susceptibility tended to be associated. He concluded that this may indicate genetic linkage, but pointed out that factors for relative maturity may simply modify resistance. No information is available concerning the relationship between resistance to the completely systemic phase of the disease common in sweet corn and the leaf blight phase observed most frequently in dent corn. Limited observations indicate that some inbred lines of dent corn are resistant to the fully systemic phase of the disease as seedlings but quite susceptible to the leaf blight phase as the plants approach maturity. More observations on this aspect of the disease are necessary before conclusions can be made. One deterrent to more intensive study of the leaf blight phase is the lack of a method for inoculating leaves that will simulate flea beetle transmission of the disease.

Control of bacterial wilt disease can be obtained through the development of resistant inbred lines and hybrids. What has been accomplished in breeding for resistance to bacterial wilt is an outstanding example of disease control in plants. Previous to 1932 the disease caused serious losses in sweet corn varieties during years when it was severe. In 1933 the hybrid, GOLDEN CROSS BANTAM, was released. This single cross, developed specifically for resistance to bacterial wilt, has since proved to be one of the most popular yellow sweet corn hybrids (Smith, 1933). A number of other sweet corn hybrids have been developed by both state agricultural experiment stations and private seed companies. Had resistant sweet corn hybrids not been available, the potentially severe outbreak of bacterial wilt in 1953 would have undoubtedly caused very serious losses. Within sweet corns, the white EVERGREEN and COUNTRY GENTLEMAN types are more resistant generally than the yellow, GOLDEN BANTAM types. In dent corn there is an apparent correlation between resistance to northern corn leaf blight and resistance to the leaf blight phase of bacterial wilt.

Some prevention of the disease may be obtained by spraying or dusting plants with DDT to kill flea beetles, but this practice must be started very soon after emergence of the seedlings and continued until plants are in tassel. Spencer and McNew (1938) studied the influence of mineral nutrition on the reaction of sweet corn seedlings to infection

by *B. stewarti*. Seedlings deficient in potassium were more severely infected than those deficient in either phosphorus or nitrogen. High applications of nitrogen induced severe wilting in infected plants. It was evident that mineral nutrition of the host exerts some influence on the host-parasite complex of bacterial wilt, but the exact changes brought about were not ascertained. How far these results would apply to older plants under field conditions is not known.

5. Rusts

Corn is susceptible to three rusts—common corn rust, southern corn rust, and tropical corn rust. In the United States only the first two

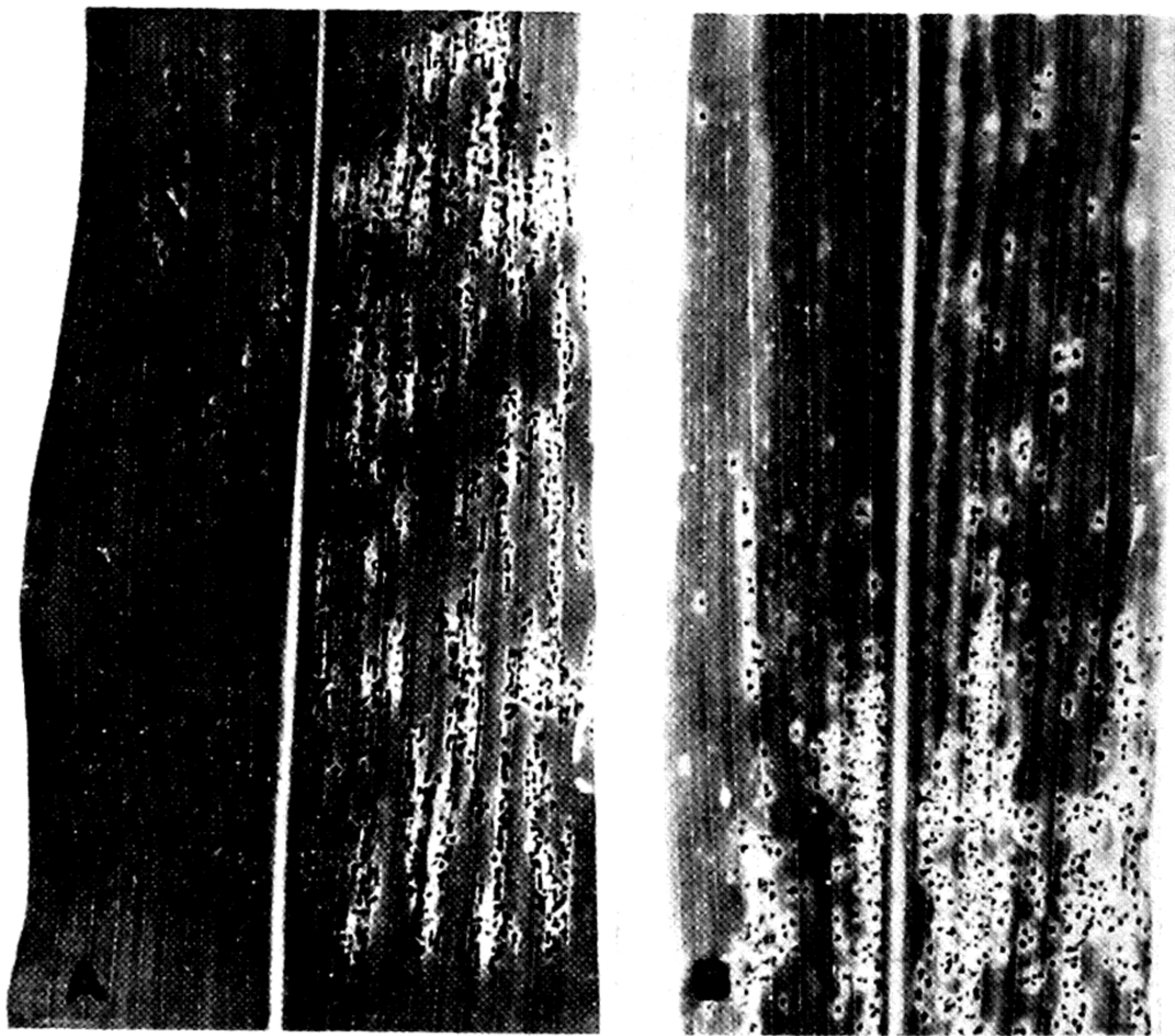


FIG. 16. A. Common corn rust. B. Southern corn rust.

have been reported. Both diseases are generally of minor importance but occasionally they may become quite abundant and cause considerable leaf killing (Wallin, 1951; McKeen, 1951c). Data of the possible effect of these diseases on grain yields are lacking. The three rusts differ from each other on the basis of the symptoms produced and morphology of the inciting agents.

Common corn rust is recognized by the circular-to-elongate, cinnamon-brown, powdery pustules (uredinia) scattered over both surfaces of the leaves (Fig. 16A). As corn matures, the pustules become brownish-black owing to replacement of red urediospores by black teliospores.

Rust pustules may appear on any of the above-ground parts of the plant, but they are most abundant on the leaves.

Puccinia sorghi is the name of the fungus inciting common corn rust. Urediospores are cinnamon-brown, globoid to ellipsoid, finely to moderately echinulate, $26-32 \times 23-29 \mu$ in size, and have 3 to 4 equatorial pores. Urediospores are spread by wind and, under favorable conditions, will continue to initiate infections on corn throughout the growing season. Each spore contains two haploid nuclei, as does each cell of the mycelium which develops in the leaf tissue following infection. As the host matures teliospores develop in the pustules. These spores are brownish-black, oblong to ellipsoid, rounded or obtuse at both ends, and measure $29-54 \times 16-23 \mu$. They are two-celled and slightly constricted at the septum, and the spore wall is thickened at the apex (Fig. 17A). Each spore is attached to a pedicel once or twice the length of the spore. Teliospores are binucleate, but before germination the two haploid nuclei fuse to form the truly diploid phase of the fungus. Teliospores germinate in the spring to form a basidium on which small, hyaline, thin-walled basidiospores are formed. With the onset of germination meiotic division of the fusion nucleus takes place. The haploid basidiospores are incapable of parasitizing corn but will infect a number of species of wood sorrel (*Oxalis*). Following penetration of leaves of susceptible *Oxalis* species, spermagonia (pycnia) are formed. These structures are inconspicuous and few in number, resembling pimple-like eruptions. Minute hyaline spores (spermatia) develop within the spermagonia and are exuded in a syrupy matrix. These spermatia, which are uninucleate and haploid, fuse with receptive structures (paraphyses) protruding from the ostioles of spermagonia. The single nucleus of a spermatium passes into a paraphysis and pairs, but does not fuse, with a nucleus in the latter. Fusion takes place only between spermatia and paraphyses originating from spermagonia of opposite mating type. By successive division and migration of nuclei, diploidization proceeds through the mycelium associated with a "fertilized" spermagonium. Without fusion between spermatia and paraphyses the mycelium within the *Oxalis* leaf remains in the haploid condition and further development of the parasite is stopped. Following diploidization, the cluster cup or aecial stage of the rust forms on the lower surface of the leaf. Aecia bear numerous binucleate aeciospores which are globoid to ellipsoid, finely verrucose, and pale-yellow, measuring $18-26 \times 13-19 \mu$. Aeciospores are carried by wind to corn leaves, where under favorable conditions they germinate and penetrate. Following infection of the corn leaves by aeciospores, urediospores are produced. Urediospores may overwinter in southern and central United States and

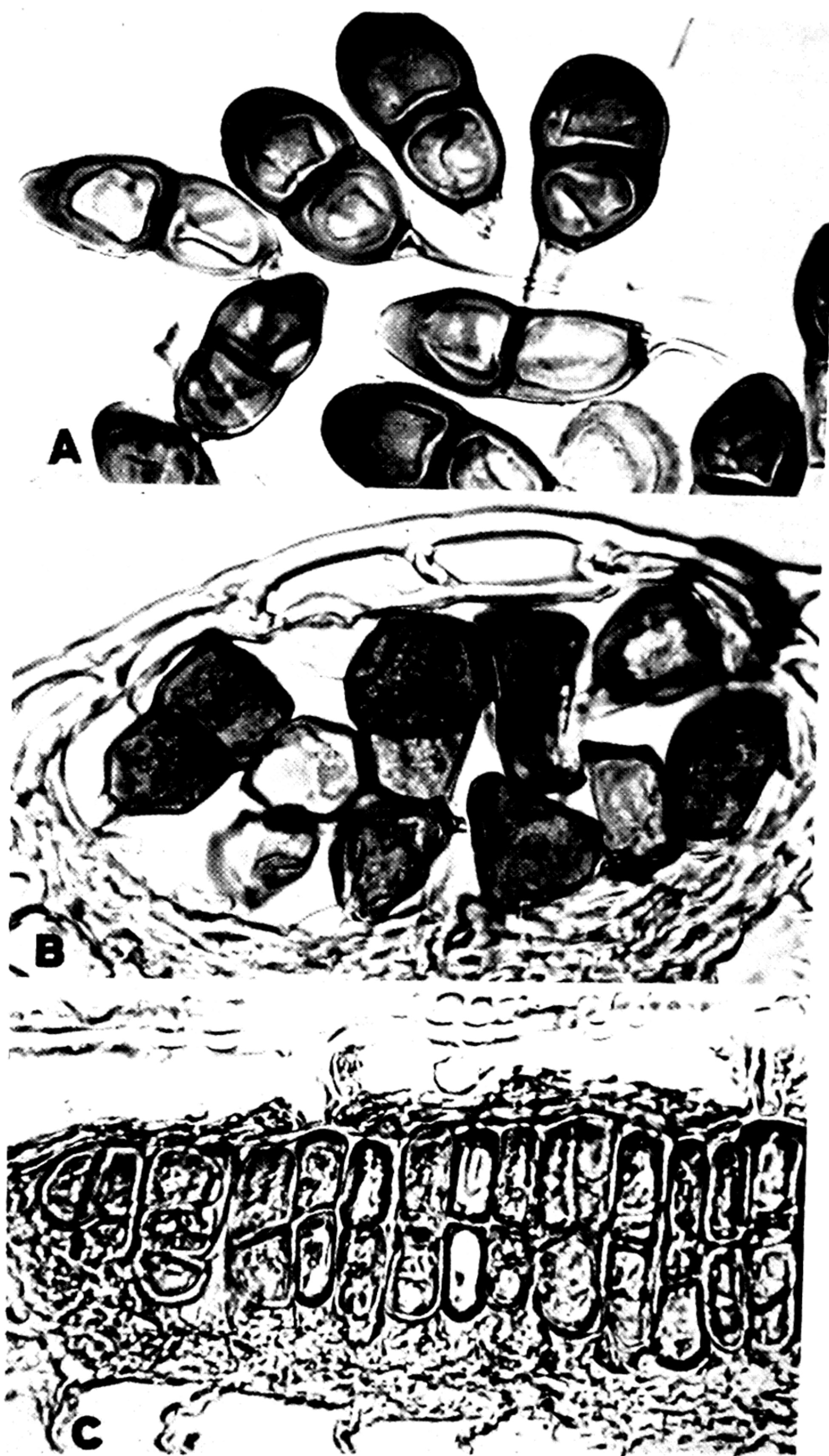


FIG. 17. A. Teliospores of *Puccinia sorghi*. B. Teliospores of *P. polysora* covered by epidermis of the leaf. Note that these spores are more angular, show less thickening at their apices, and have shorter pedicels than those of *P. sorghi*. C. Teliospores of *Angiopsora zeae* covered by epidermis of the leaf. Note concatentate arrangement and lighter color of these unicellular spores. (Courtesy of Dr. G. B. Cummins, Department of Botany and Plant Pathology, Purdue University.)

serve as initial inoculum on corn in the spring, thus bypassing the necessity of the alternate host, *Oxalis*, in the life cycle of the fungus. Where this occurs, urediospores may be carried progressively northward as the growing season advances and furnish the bulk of primary inoculum of corn rust in the Corn Belt. Heterothallism of *P. sorghi* was first described by Cummins (1931). By ingenious means he proved the vital role of spermatia in diploidization. Allen (1933, 1934), in a cytological study of the function of the spermatia, verified the findings of Cummins. She pointed out also that diploidization might possibly take place by anastomosis between haploid hyphae within the *Oxalis* leaf, or by fusion of germ tubes of germinating spermatia with haploid mycelium often present in the stomatal openings of the leaf.

Differences in resistance to common corn rust are apparent among inbred lines. Mains *et al.* (1924) found rust reaction to range from near immunity to complete susceptibility within a large group of inbred lines. In later studies Mains (1926) identified four physiologic races within *P. sorghi* on the basis of their pathogenicity on certain inbred lines. Stakman *et al.* (1928) detected seven physiologic races of the pathogen. Mains (1931) found resistance to both race 1 and race 3 to be determined by a single dominant gene. In certain other inbred lines, resistance to race 1 depended upon a single dominant gene which was apparently distinct from the gene governing resistance to both races. Linkage studies by Rhoades (1935) indicate the gene for resistance to race 3 to be located in the short arm of chromosome 10.

Cool temperatures and high relative humidity favor spread and development of common corn rust. Weber (1922) observed the minimum temperature for germination of urediospores to be near 4°C., the optimum about 17°C., and the maximum near 32°C. McKeen (1951c) obtained excellent germination of urediospores over a range of 13° to 27°C. but none at 31°C. Studies conducted by Smith (1926) show that at 25°C. best germination of urediospores was obtained at 100 per cent relative humidity, and only 3 per cent germination was obtained where the relative humidity was lowered to 97.5 per cent.

Southern corn rust has been known in the United States for a considerable period of time (Cummins, 1941). It is found chiefly in the southeastern states, but may range as far north as Massachusetts and southern Indiana. Recently the disease has become important in Africa (Nattrass, 1953; Rhind *et al.*, 1952). This disease and common corn rust are quite similar in appearance. The light cinnamon-brown pustules of southern corn rust tend to be somewhat smaller and more circular than those of common corn rust (Fig. 16B). Telia are chocolate-brown to black, circular to elongate, and distinguished from those

of common corn rust by retention of the leaf epidermis over the pustules for a long time.

Puccinia polysora is the name of the fungus inciting southern corn rust. Urediospores are yellowish to golden, globoid, and finely and sparingly echinulate, measures $29-36 \times 23-29 \mu$, and have four to five indistinct equatorial pores. Teliospores, distinguished readily from those of *P. sorghi*, are chestnut-brown, angular, irregularly ellipsoid or ovoid, and $29-41 \times 20-27 \mu$ in size (Fig. 17B). The spores are two-celled and slightly constricted at the septum, and the apical wall is only slightly thickened. Each spore is borne on a short pedicel one-fourth or less the length of the spore. Southern corn rust differs from common rust in that no alternate host is known; consequently aecial and pycnial stages have not been described.

Southern corn rust appears to require somewhat higher temperatures than common corn rust for optimum development. This is suggested by its geographic range in the United States and its prevalence in warmer areas in the Western Hemisphere. It is of interest to note that Nattrass (1953) observed that southern corn rust in Kenya was confined to the warm, low-lying humid areas, whereas common corn rust was present in the cool humid climate at higher altitudes.

Little has been published on the disease other than notes on its occurrence and mycological descriptions. Information regarding the reaction of inbred lines to the disease or the possible existence of physiologic races within the species is wanting.

Tropical corn rust is found in the warm humid areas of the Western Hemisphere. It has not been reported from the United States. The inciting agent *Angiopsora zeae* was first described by Mains (1938). Uredinia, which occur mainly on the upper surface of leaves are 0.3 to 1.0 mm. in size, pale yellow, and covered by the epidermis of the leaf except for a small pore or slit. Urediospores are ovoid, colorless to yellowish, and moderately echinulate, measuring $22-34 \times 16-20 \mu$. Telia, found usually encircling the uredinia, are chocolate-brown and long covered by the epidermis. Teliospores are golden-brown, one-celled, angular, oblong, borne in sessile chains of two spores, and measure $16-28 \times 12-18 \mu$ (Fig. 17C). No alternate host for this rust is known.

6. Brown Spot

Brown spot or physoderma disease of corn is often prevalent in the South Atlantic and Gulf Coast states. It has been found as far west as Kansas and northward into South Dakota.

Symptoms of the disease are seen mainly below the ears on leaves,

leaf sheaths, and stalks. The first indications of infection appear as bleached, yellowish spots which later turn brown. At this stage symptoms resemble slightly those of common corn rust. The spots coalesce to form larger blotches especially at the base of the leaf blades and on adjoining tissue of the leaf sheaths (Fig. 18A). Infections on the leaf sheaths may be mistaken for purple sheath spot. Stalks become infected at the nodes beneath the sheaths. Cells of infected tissue eventually break down, exposing pockets of dusty, reddish-brown spores of the

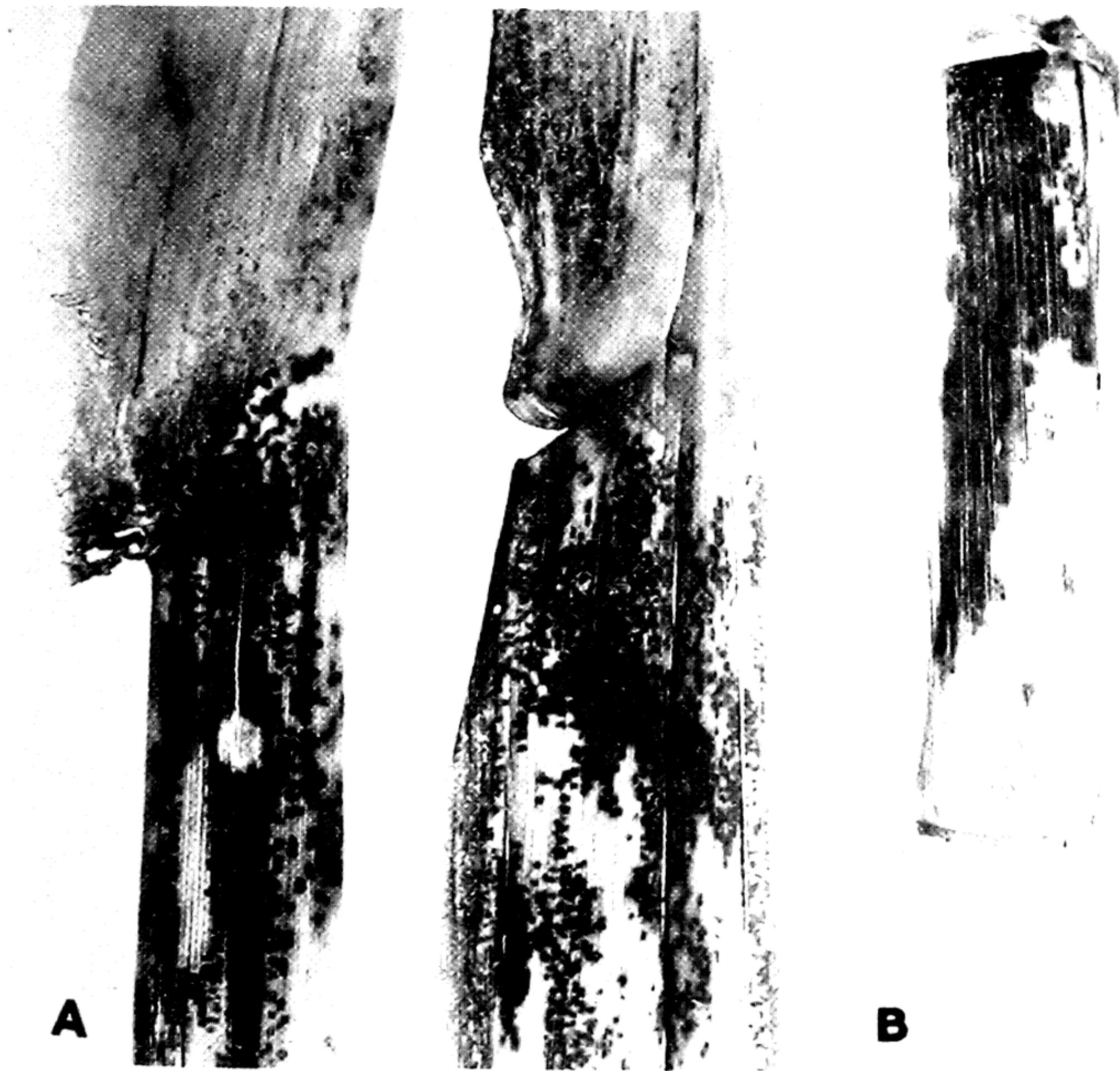


FIG. 18. A. Brown spot disease. B. Purple sheath spot. (Fig. 18A from Tisdale, 1919.)

fungus. In severe cases of infection all of the leaves and leaf sheaths become diseased and die prematurely. Severely infected stalks break over at the nodes.

The fungus inciting this disease, *Physoderma zeae-maydis*, is relatively simple in structure. Sporangia, which are produced in abundance in invaded host cells, are smooth, brown, thick-walled, $20-30 \times 18-24 \mu$ in size, and generally globe-shaped, except for a flattened area on one side. When sporangia germinate, a cap or lid opens to release a thin-walled endosporangium which ruptures and liberates a number of uniciliate zoospores. Occasionally multiciliate zoospores have been observed (Ojerholm, 1934). Zoospores are $5-7 \times 3-4 \mu$ in size, with the cilium

three to four times the length of the spore. These motile spores eventually come to rest on the leaf surface, round up, lose their cilia, and send out fine infection hyphae which penetrate the host tissue. Sparrow (1934) observed that after the zoospores come to rest they develop into irregular, slipper-shaped structures of varying size, which are anchored to the host by a coarse branched rhizoidal system. At maturity these extramatrical, thin-walled sporangia release great numbers of zoospores which are capable of infecting other host cells. The zoospores are similar to those produced by the thick-walled resting sporangia except for being much smaller. After infection has been established, large vegetative cells are formed within the network of the fine mycelial strands inside the host. These enlarged cells, which may occur singly or in groups, produce sporangia directly or may send out short pedicels on which terminal sporangia are borne. Parasitized host cells ultimately die and release the mature, reddish brown sporangia.

Germination of sporangia takes place in the presence of free water and at relatively high temperatures. Tisdale (1919) found germination to be best in the range of 23° to 30°C., with an optimum of about 28°C. In a study of factors affecting germination Voorhees (1933b) observed that direct sunlight was lethal to the sporangia and that no germination occurred in complete darkness. Sporangia remained viable after two years of storage in the laboratory and germinated well after exposure for one month to temperatures of either 0°C. or 70°C. Exposure to 80°C. for the same period was lethal.

Eddins (1933) studied the host range of the fungus and found all types of *Zea mays* to be susceptible. The only other host among a number of grasses tested was *Euchlaena mexicana*. Differences in resistance to brown spot were observed between inbred lines of corn. None, however, was immune. Kelman and Herbert (1952) also reported marked variation in reactions to the disease among inbred lines. They were able to successfully inoculate corn plants about 3 feet high, using either dry sporangia or a water suspension of the latter placed in the whorl.

Control of brown spot of corn will probably come through development of resistant inbred lines. Some progress has been made in this respect in some of the southern states. Crop rotation and sanitation are not effective in practical control of the disease.

7. Bacterial Leaf Blight and Stalk Rot

Bacterial leaf blight was first reported in the United States about 25 years ago (Johnson *et al.*, 1929). Since that time it has been seen in a number of southern and central states (Pady, 1943; Slagg, 1944; Johnson *et al.*, 1945). The disease appears to be confined to the United States,

although a similar disease has been described by Ludbrook (1942) in Australia. Bacterial leaf blight has thus far been of minor importance, except for a few severe outbreaks in localized areas.

Symptoms on the leaves appear as well-defined, narrow elliptical lesions ranging in size from spots 1 to 2 mm. long, up to necrotic stripes 400 mm. or more in length (Fig. 19). Lesions may coalesce to form extensive necrotic areas which later become shredded. At first lesions



FIG. 19. Bacterial leaf blight and stalk rot. *A*. Early stage of leaf infection. *B*. Stalk infection. Note rotting of stalk and top of plants and the multiple ear formation. (Figure 19*B* from Johnson *et al.*, 1949.)

appear water-soaked or translucent; later they become dry and necrotic with tan centers and narrow brownish margins. Stalks usually become infected just above the point of ear attachment where a dark-brown discoloration occurs. Extensive stalk rotting results in death of the top of the plant (Fig. 17*B*). Severely diseased plants are often stunted and show multiple ear development. Such ears are frequently sterile and may show evidence of rotting.

Pseudomonas alboprecipitans is the name of the bacterium inciting this disease. The organism is rod-shaped, Gram-negative, about

$0.6 \times 1.0 \mu$ in size, occurring singly or in chains up to 10 cells long, and motile by a single polar flagellum. On nutrient dextrose agar colonies are small, smooth, and pale-white in reflected light to slightly opalescent in transmitted light. The optimum growth of the organism is at about 30°C . The organism was first described by Rosen (1922b), who isolated it from *Setaria lutescens*. The work of Johnson *et al.* (1949) has shown that the organism on corn is identical with that described by Rosen in respect to its host range, and cultural, physiological, and morphological characters. The bacterium has been shown to be capable of entering and infecting uninjured leaves of corn, oats, wheat, barley, rye, and *Setaria lutescens* (Johnson *et al.*, 1949). Under field conditions only corn and *Setaria lutescens* have been reported as natural hosts.

Bacterial leaf blight can be distinguished from bacterial wilt on the basis of symptoms. Lesions of the latter are often wider, have wavy margins, and are not quite so sharply defined. The water-soaked, translucent aspect of lesions of bacterial leaf blight is more pronounced than that observed in bacterial wilt. The appearance and location of the stalk rot phase of the two diseases are distinctly different. The inciting organisms of the two diseases are readily separable on the basis of colony color; those of *Bacterium stewarti* are yellow, those of *Pseudomonas alboprecipitans*, white.

Because the disease is of such minor importance, no studies have been conducted on possible means of control. The writer observed rather striking differences in resistance to the disease among inbred lines under conditions of both natural and artificial inoculation.

8. Other Leaf Diseases

A few other leaf diseases of corn have been described as occurring in the United States. These are found infrequently and are of little economic importance.

Purple sheath spot is one of these diseases. Irregular, purplish-brown spots of varying size develop on the outer surface of the leaf sheaths (Fig. 18B). Beneath these spots the inner surface of the sheath is discolored and necrotic. The disease becomes conspicuous usually after silking and is almost universally present on corn. Purple sheath spot is sometimes mistaken for brown spot because of its superficial resemblance to the latter. Durrell (1920) isolated a number of species of bacteria and fungi from necrotic sheath tissues. He concluded that these organisms lived saprophytically on debris that collected behind the sheath and that later they became mildly parasitic and invaded the host tissue. Some inbred lines and hybrids show more pronounced

symptoms of purple sheath spot than others. There is no evidence that the disease causes appreciable injury.

Holcus bacterial spot of corn was first described by Kendrick (1926). The disease on corn leaves is manifest as round to elliptical spots, ranging up to 10 mm. in diameter. At first the spots are dark-green and water-soaked; later they become dry and brown with a reddish-brown margin. The disease attacks Johnson grass, Sudan grass, pearl millet, broom corn, and yellow foxtail grass. The inciting organism, *Pseudomonas syringae* (*Pseudomonas holci*), is a short rod-shaped bacterium, $0.75 \times 2 \mu$ in size, and motile by 1 to 4 polar flagella. On nutrient dextrose agar, colonies are small, round, and grayish-white. Invasion of the host takes place through stomata. The disease is of no economic importance.

Zonate leaf spot of corn occurs in the Gulf Coast states. Lesions are at first reddish-brown and water-soaked. As they enlarge, up to several centimeters in diameter, they show a very definite target-like or zonate pattern. Bain and Edgerton (1943) described the disease first on sorghum, but sugar cane, Sudan grass, and Johnson grass are hosts also. The conidia of the inciting agent, *Gleocercospora sorghi*, are hyaline, filiform, $85 \times 2.5 \mu$ in size, and borne in a slimy, salmon-colored matrix.

A leaf spot of corn, found in Mississippi, was described by Young *et al.* (1947). Lesions are $1-2 \times 2-5$ mm. in size, oval-shaped, and straw-colored. They isolated *Helminthosporium rostratum* from infected tissue and reproduced the disease on corn seedlings using pure cultures of the fungus. The pathogen also attacks pearl millet and sorghum.

Cercospora leaf spot of corn and the inciting fungus, *Cercospora zeae-maydis*, were described first by Tehon and Daniels (1925). Spots are gray to tan, narrow, and 0.5×12 cm. in size. The conidia of the fungus are hyaline, $30-80 \times 5-9 \mu$ in size, and multiseptate. Hyre (1943) and Roane (1950) have reported the disease in abundance in Kentucky, Tennessee, and Virginia. A somewhat similar disease found also in southern United States is incited by *C. sorghi*. This species has narrower and longer spores.

Anthracnose of corn is occasionally found in this country. Roane (1950) reported a localized outbreak of this disease on sweet corn in Virginia. The fungus inciting the disease is *Colletotrichum graminicola*.

VI. Corn Smuts

Corn is susceptible to two smuts. Common smut, or boil smut, is widely distributed throughout the world in nearly every area where

corn is grown. Head smut, of minor importance in the United States, is found in the western states and very rarely east of the Great Plains. The disease is more prevalent in Europe, Asia, Africa, and Australia than in this country.

1. Common Smut

The incidence of common smut in the United States varies from year to year and from one location to another. In the Corn Belt estimates of loss due to the disease range from a trace to 6 per cent. It is doubtful if losses exceed 2 per cent over very wide areas. In sweet corn,



FIG. 20. Common smut of corn. A. Tassel infection. B. Young gall involving the entire ear. Note the white glistening appearance of the outer membrane of the gall. Chlamydospores have just begun to develop in the interior. C. Fully developed gall on an ear showing black powdery masses of chlamydospores.

however, losses may be much higher. The number, size, and location of the galls determine the amount of damage. Immer and Christensen (1928b, 1931) and Johnson and Christensen (1935) found large galls and galls above the ear to be more destructive than small galls or galls below the ear. This same general relationship between size and location of galls and yield reduction was observed by Smith (1936). Garber and Hoover (1928), however, concluded that the only significant losses were those resulting from barrenness induced by smut. Where smut did not cause barrenness, they were unable to demonstrate yield reductions.

Symptoms of common smut are usually conspicuous and easily identified. All of the above-ground parts of plants are susceptible. Galls are at first covered with a glistening whitish membrane (Fig. 20B)

that later ruptures and exposes a mass of powdery black spores (Fig. 20C). Galls on leaves seldom develop beyond the size of a pea; they usually become dry, hard, and warty and contain few spores. Meristematic tissue is especially vulnerable to attack, and ears, tassels (Fig. 20A), and nodal buds are most often infected because of the abundance of such tissue in these parts. Early infection may cause dwarfing and death of young plants, but galls on seedlings in the field are seldom seen.

Ustilago maydis (*U. zae*) is the fungus inciting common smut. Chlamydospores are brownish-black, thick-walled, heavily echinulated, oval to spherical in shape, and 8 to 12 μ in diameter. Germination of chlamydospores is attended by the formation of a septate promycelium on which small, thin-walled, single-celled, ellipsoid sporidia are borne. Variations from this normal type of germination are occasionally observed in which sporidia may develop directly from the chlamydospore, branching of the promycelium may take place without formation of sporidia, or more than one promycelium may arise from a chlamydospore (Kernkamp and Petty, 1941). Growth of the fungus on artificial media is composed of mycelial strands and sporidia; chlamydospores do not develop—they are formed only in host tissue. Sporidia increase in number by budding. The fungus is composed of numerous races which arise by mutation or as a result of combination and segregation following hybridization between compatible mating types (Christensen, 1929; Stakman *et al.*, 1933). Sporidia are generally uninucleate and haploid, and those of opposite mating type fuse to form a binucleate thallus (Sleumer, 1932; Bowman, 1946). Occasionally reduction division of the diploid or fusion nucleus of the chlamydospore is delayed so that diploid sporidia are formed and haploid sporidia do not appear until the following chlamydospore generation (Chilton, 1940). Fusion of haploid, uninucleate sporidia is normally necessary before the fungus can incite typical symptoms in the host. Sometimes cultures derived from a single sporidium are capable of inciting typical gall formation. Such so-called “solopathogenic” cultures are presumably diploid because of failure of reduction division of the fusion nucleus during germination of the chlamydospore (Christensen, 1931).

Germination of chlamydospores takes place in the presence of free water and between 8° and 36°C.; the optimum range is between 26° and 34°C. (Jones, 1923; Huttig, 1931). Sporidia are carried by wind to the host. Penetration of meristematic tissues may take place by binucleate infection hyphae which develop following sporidial fusion, or by infection hyphae arising directly from germinating chlamydospores (Walter, 1934). Invasion of the host may be direct (Walter, 1934) or

through stomata or wounds (Kornfeld, 1937). The parasitic mycelium stimulates host cells to increase in size and number, resulting in gall formation. Ultimately chlamydospores develop in the mycelium in the galls. Davis (1936) presented evidence suggesting that *U. maydis* may develop systematically in the host, with gall formation taking place as the host tissues differentiate during the growing season. It was pointed out that expression of infection was influenced by host development and that some infections never become apparent as typical galls. It is generally believed that most galls form as a result of local infection. Piemeisel (1917) and Itzerott (1938) found no evidence of systemic invasion by the fungus. Scurti (1949, 1950) found young galls devoid of mycelium, but after a lapse of time hyphal strands of the fungus were observed. He suggests that the initial response of host cells is stimulated by a substance that diffuses some distance from the parasitic mycelium.

The epidemiology is not well understood. Piemeisel (1917) concluded that high humidity favored smut infection, but most reports in the literature indicate dry warm weather to be conducive to the development of this disease (Potter and Melchers, 1925; Coffman *et al.*, 1926; Immer and Christensen, 1928a; and Platz, 1929). It has not been determined whether dry warm weather predisposes the host to infection or provides more favorable conditions for dispersal and growth of the fungus.

Other environmental factors appear to influence the prevalence of common smut. Plants grown on soil exceptionally high in nitrogen or on soils where heavy applications of barnyard manure have been made often show a high incidence of the disease. Whether this is an influence on the host or on the parasite has not been determined. Injury due to hail or injuries resulting from cultivating machinery increase the amount of smut, presumably by exposing to invasion tissues which would otherwise be protected. Detasseling corn in seed fields often results in the production of galls at nodes where tassels are removed. Menzies and Stanberry (1947) found as high as 22 per cent reduction in yield due to smut that was induced by detasseling.

Growth characteristics of the host may influence susceptibility to smut. Kyle (1929) observed a much higher incidence of ear smut on plants with poor husk coverage than where ears were well protected by the husks. Exceptionally vigorous segregates tended to show more smut than those of less vigor (Kyle, 1930).

The most effective means of controlling smut appears to be through breeding and selection. Stringfield and Bowman (1942) have pointed out that many inbred lines used in the Corn Belt have a reasonable de-

gree of resistance to smut as well as desirable agronomic characters. Jones (1918) observed marked differences in smut resistance between strains of corn. These findings have since been verified by Hayes *et al.* (1924); Garber and Quisenberry (1925); Immer and Christensen (1931); and Johnson and Christensen (1935). In crosses between resistant and susceptible inbred lines the F_1 is generally intermediate in reaction to smut infection (Immer, 1927; Hoover, 1932). In a few instances Immer found susceptibility to be dominant. Linkage studies by Hoover (1932), Burnham and Cartledge (1939), and Saboe and Hayes (1941) indicate that resistance to smut infection is determined by a large number of genes.

Control of smut through crop rotation and by destruction of smut galls has been recommended, but it is doubtful if these methods would be particularly effective where corn is extensively grown. Destroying smut galls as a control measure is obviously impractical except perhaps in small garden plots. Pepper and Haenseler (1944) reported an interesting case of smut control following the application of rotenone and nicotine to sweet corn for control of insects. The reason smut was reduced by the use of insecticides is not clear. The authors suggest that insects may, through feeding injuries, open up avenues of invasion for the pathogen.

2. Head Smut

Head smut of corn was first reported in this country in 1895. The disease is unimportant, and only in rare instances have local outbreaks been serious. Head smut of sorghum, incited by the same fungus, is somewhat more prevalent.

The first symptoms of head smut of corn become evident when tassels and ears appear. These parts may be partly or completely converted to spore masses. Galls are at first covered with a membrane which soon breaks open to expose a powdery, black mass of spores and the vascular bundles of the host. The network of conductive tissue in the galls distinguishes this disease from common smut. When tassels or ears are only partly converted to galls, it is not uncommon to find a leafy proliferation of the floral bracts. Little or no stunting is evident in infected plants.

Spacelotheca reiliana is the inciting agent of head smut. Chlamydospores are brown to black, thick-walled, spherical to slightly irregular in shape, and 9 to 12 μ in diameter. Chlamydospores germinate to form a septate promycelium bearing small, hyaline, thin-walled, single-celled sporidia. Penetration of young germinating corn seedlings takes place following fusion of haploid sporidia of compatible mating type

to form binucleate infection hyphae. The parasitic mycelium develops systematically in the host tissue, and galls are formed after ears and tassels appear (Potter, 1914). The morphology and life cycle of the fungus are not greatly different from those of *Ustilago maydis*. Seedling infection and completely systemic development of the mycelium in the host are features which markedly distinguish the two diseases. Reed *et al.* (1927) have demonstrated two races within *S. reiliana*, one of which infects corn, the other, sorghum; some cross infection was observed under experimental conditions.

Very little is known regarding factors influencing disease development. Christensen (1926) found that infection took place over a rather wide range of temperatures, and that dry soil was more favorable for invasion of the host than wet soil.

Because of the minor importance of the disease not much is known regarding the resistance of inbred lines. Seed treatment is somewhat effective in destroying seed-borne spores of the organism but will not protect seedlings against infection in smut-contaminated soil (Bressman and Barss, 1933). Seed treatment and crop rotation are recommended as partial control measures.

VII. Miscellaneous Diseases

The corn diseases described under this heading are grouped together for no reason except convenience. They do not fit easily into the other broad classes of diseases listed above. The only characteristics they have in common are the general systemic invasion of their hosts and their relatively minor economic importance in the United States.

1. Virus Diseases

Four virus diseases are known to occur on corn under natural conditions in the United States. The virus diseases of corn in this country have not caused appreciable damage to the crop, and none is present in the Corn Belt. Other more serious virus diseases of corn are found in Hawaii, the West Indies, Africa, and Australia.

Sugar-cane mosaic appears to be the first virus disease recognized on corn in this country. It was described by Brandes (1920) under the name corn mosaic. Kunkel (1927) showed, on the basis of specificity of insect vectors, that the two diseases are distinct. Corn mosaic occurs in Hawaii, Africa, and the West Indies, but not in the United States. Sugar-cane mosaic of corn is found in the Gulf Coast states where the crop is grown in the vicinity of sugar-cane. Symptoms appear as streaking and irregular mottling of the leaves. Upper leaves are often yellow-

ish-green. Little if any stunting occurs, but in severe cases of infection partial or complete sterility of ears is found. The disease is not transmitted through seed. The disease has an extensive host range within the *Gramineae*, and is readily transmitted by the corn aphid, *Aphis maidis*. Other aphids, *Toxoptera graminum* and *Hysteroneura setariae*, are capable also of transmitting the virus. Mechanical transmission can be accomplished with little difficulty. Stoneberg (1927) studied the effect of sugar-cane mosaic on corn in Louisiana and concluded that, although the disease had some deleterious effect on yield and quality, it could not be considered of major importance in reducing corn yields. Introduction of resistant varieties of sugar cane has reduced the incidence of the disease on corn.

Another virus disease on corn in this country is celery stripe, which is incited by the southern celery-mosaic strain of cucumber mosaic virus. Wellman (1934) noted that *Commelina nudiflora* was an important reservoir of the virus under field conditions. In a further study of the host range among monocotyledonous plants, Wellman found corn, wheat, rye, sorghum, and teosinte to be susceptible. Subsequently the disease was found occurring naturally on corn in widely separated fields in Florida. *Aphis gossypii* is the natural vector of the virus, but transmission may also be accomplished by mechanical inoculations with infective plant juice. The distinction between celery stripe and white stripe of corn found in Cuba is based in part on the inability of *Peregrinis maidis*, the vector of white stripe, to transmit celery stripe. Symptoms are first apparent as small spots about the insect punctures which soon enlarge and elongate. Evidence of systemic infection is observed in the longitudinal light-colored streaks on the leaves. Marked stunting accompanies severe infection. Chlorotic patterns may develop as plants become older, and darkening of the vascular bundles in the stalk has been noted. The disease appears to be confined to Florida, and there is no evidence that it causes any appreciable losses in corn.

Corn stunt was found first in the San Joaquin Valley in California in 1942 (Frazier, 1945). Alstatt (1945) and Pickett *et al.* (1946) reported a similar disease in the Rio Grande Valley of Texas. The relationship between the disease in California and the disease in Texas was not established until Kunkel (1946) proved them to be incited by the same virus. One of the most striking symptoms of stunt in the field is the abnormal extension of nodal buds below the ear to give plants a bushy appearance. These lateral branches may be 2 to 3 feet long. Many plants are dwarfed owing to shortening of internodes. Where infection takes place early, all nodes are so affected, whereas later infection brings about shortening of internodes only above the ear. Leaves

are light-green and often streaked (Fig. 21) with etiolated bands; sometimes the margins and tips are red or bronze colored. Prolificacy is a common symptom, and ears are often small and only partially filled. The disease is not seed-borne. Kunkel (1946, 1948) demonstrated that the virus could not be transmitted mechanically, but that the leaf hopper, *Baldulus maidis*, was an efficient vector. The minimum



FIG. 21. Corn stunt. Note bushy appearance of the plant and striping of the leaves. (Courtesy of E. V. Walter, United States Department of Agriculture.)

incubation period of the virus in the vector was found to be 14 days. The minimum time elapsing between inoculation and the appearance of symptoms in the host was 26 days. A second species, *Baldulus elimatus*, has been demonstrated as a vector of the virus in Mexico (Niederhauser and Cervantes, 1950).

Leaf fleck, the fourth virus disease known on corn in this country, was discovered by Stoner (1952). The first symptoms appear as small, circular, pale spots near the tips of the oldest leaves. The spots enlarge

to about 2 mm. in diameter and become yellowish. The tips and margins of the leaves show burning as the disease progresses. Symptoms advance from lower to upper leaves until the entire plant is flecked. The only other host is Harding grass (*Phalaris tuberosa*). The virus is not transmitted through seed. Three species of aphids have been demonstrated as vectors; these are *Rhapalosiphum prunifoliae*, *R. maidis*, and *Myzus persicae*. The time elapsing between inoculation and appearance of symptoms is reported to be about six weeks. Mechanical transmission of the virus is not successful.

2. Downy Mildews

Corn is susceptible to seven downy mildew diseases. Two of these are known to occur in the United States and will be described below; the remaining five are distributed in the Eastern Hemisphere, particularly in India, Southeast Asia, Philippine Islands, Indonesia, and Africa. All of the diseases are incited by distinct species of the genus *Sclerospora*. All members of the genus are obligate parasites. The downy mildews of corn show some similarity to one another in symptoms. Chlorotic streaking and mottling, stunting, malformation of the ears and tassels, and excessive tillering are general symptoms often associated with these diseases. Systemic infection is a characteristic of all downy mildews of corn.

The disease known in the United States as downy mildew of corn is exceedingly rare. According to Weston (1929), the first observation of this disease in the United States was made by R. B. Streets, who found it on sweet corn in Wisconsin in 1921. Melhus *et al.* (1928) report only two instances of natural occurrence of the disease on corn in Iowa. Symptoms of the disease on corn are described by Melhus *et al.* (1928) as grayish blotching and mottling of the leaves, which may extend over the entire plant. In many cases chlorotic streaking of the leaves is evident. Stunting and a bushy, stocky appearance, due to shortening of the internodes, are characteristic of infected plants. *Sclerospora graminicola* is the fungus inciting downy mildew of corn in this country. Sporangiophores are stocky, irregularly branched, hyaline, and average about $270\ \mu$ in length. Sporangia are hyaline, oval- or lemon-shaped, and $14\text{--}23 \times 11\text{--}17\ \mu$ in size. Mature sporangia have a papilla of dehiscence prominent at the apex. Germination takes place by the release of 3 to 12 or more kidney-shaped biciliate zoospores. Oöspores have not been observed in corn but are abundant in the tissues of infected *Setaria*. They are thick, rough-walled, reddish-brown, globose, and $30\text{--}60\ \mu$ in diameter. Oöspores germinate directly to form a germ tube. Melhus *et al.* (1928) infected germinating corn seedlings by placing mature

oöspores, gathered from infected *Setaria* leaves, in contact with corn seed. Sporangia were produced in abundance on leaves of corn seedlings held in a humid atmosphere. These sporangia incited the disease when transferred to healthy plants under moist conditions. The optimum temperature for infection ranged between 14° and 18°C. Species of *Euchlaena*, *Holcus*, *Zea*, *Saccharum*, and *Setaria* are susceptible. In the United States *Setaria viridis* is the most commonly observed plant attacked by the disease.

Crazy top is the only other disease of corn in the United States incited by a species of *Sclerospora*. This disease occurs sporadically and is known to be distributed from New York to Wyoming and southward to Kentucky. It is of very little economic importance. The most conspicuous symptom of crazy top is the partial or complete proliferation of the tassel (Fig. 22A, C). This witch's broom condition is due to the replacement of normal floral structures by small leaves. Excessive ear shoots on the stalk and an increased number of internodes above the ear and in the ear shank are often observed. Marked stunting, narrow leathery leaves, excessive tillering, and complete suppression of tassels and ears often characterize severely affected plants (Fig. 22B). The straplike leaves are often roughened on their lower surfaces as are leaf sheaths (Fig. 22D). Longitudinal, translucent, or chlorotic, streaking is often evident in stunted plants (Fig. 22E, F). Most diseased plants are barren, but a small percentage of them may bear nubbins with a few kernels. Many gradations of symptoms are to be found from nearly normal plants with slight tassel proliferation to severely stunted plants with straplike leathery leaves. *Sclerospora macrospora* appears to be the inciting agent of crazy top. In early descriptions of the disease in this country (Koehler and Holbert, 1930; Koehler, 1939) no organism was found associated with the affected plants. Later, in a detailed histological examination of tissues of plants showing symptoms of all degrees of severity, Ullstrup (1952) found the fungus *Scl. macrospora* associated consistently with the diseased condition. The mycelium was intercellular and systemic, although very sparsely distributed in plants with mild symptoms. Oöspores were very abundant within the leaves and leaf sheaths of severely affected plants. Sporangia were not found, but recently the writer has observed them on one corn plant affected with the disease. The sparsity of development of the fungus in mildly affected plants may be one reason why, for many years in this country, the inciting agent of crazy top was not recognized. It is worthy of note that in Italy, Cugini and Traverso (1902) described a disease identical with crazy top and found *Scl. macrospora* in the affected tissues. The identity of the fungus is based largely on the oöspores, which are thick-



FIG. 22. Crazy top of corn. *A.* Typical "witch's broom" appearance of the tassel. *B.* Severely infected plants. Note stunting, tillering, narrow, straplike leaves, and failure of tassels to develop. *C.* Different manifestations of phyllody of the tassel. *D.* Rough warty surface of infected leaf sheath. *E.* Narrow, leathery, striated leaf. *F.* Longitudinal streaks on leaf.

walled and yellowish and range from 42 to 75 μ in size. Peyronel (1929) observed lemon-shaped sporangia emerging from stomata of wheat leaves infected with the fungus. Peglion (1930) found oöspores to germinate by the formation of sporangia. Sporangia germinated to release biciliate zoospores. Recently Thirumalachar *et al.* (1953) observed sporangia in moderate numbers on infected leaves of *Eleusine coracana*.

These were lemon-shaped and $60\text{--}100 \times 43\text{--}64 \mu$ in size, with one to five of them borne on simple sporangiophores 10 to 15μ in length. The sporangia germinated by release of 24 to 32 kidney-shaped biciliate zoospores. On the basis of morphology of sporangiophores and sporangia, and the mode of germination of oöspores (observed by Peglion, 1930) these authors have erected a new genus *Sclerophthora* and have reduced *Sclerospora macrospora* to a synonym of *Sclerophthora macrospora*. In this country the host range of the fungus includes corn, wheat, oats, and barley as well as the following wild grasses: crab grass, goose grass, green foxtail, witch grass, barnyard grass, and love grass. Nothing is known of the resistance of inbred lines or hybrids of corn to this disease. Attempts to artificially inoculate healthy corn with crazy top have been unsuccessful (Ullstrup, 1952). No case is known to the writer where the disease has been induced in any of its hosts by artificial inoculation. The disease may be seed-borne, but this fact is unimportant in its spread in the United States. The primary factor determining the occurrence of crazy top appears to be flooding or waterlogging of the soil between planting and when seedlings are about 6 to 8 inches high. The disease has not been found where this condition did not prevail. The fact that the disease does not occur invariably following waterlogging suggests that other factors such as temperature, duration of waterlogging, and age of seedlings are important in determining infection.

3. Black Bundle Disease

The so-called black bundle disease of corn was first intensively studied by Reddy and Holbert (1924), who considered it to be of general occurrence throughout the United States. In a survey conducted in central Illinois over a three-year period they noted the average annual incidence of the disease to be about 6.5 per cent. Koehler and Holbert (1930) reported 70 per cent of the plants affected in some fields, and estimated the average annual loss due to this disease in Illinois to be about 3 per cent. Reddy and Holbert (1924) found yield reductions of over 19 per cent in plots grown from seed selected from plants showing symptoms of black bundle disease. Symptoms of the disease become evident usually when corn has reached the dough stage or later. One of the first indications of the disease is purpling of stalks and leaves. Very often such plants are barren or bear only nubbins. Other symptoms are prolificacy, excessive tillering, and multiple ears. Positive indication of the disease is the blackening of the vascular bundles observed when stalks are cut open. Any one or a combination of these symptoms may appear in a single plant. *Cephalosporium acremonium* is considered to be the inciting agent of black bundle disease. Spores of

the fungus are hyaline, single-celled, oval-shaped, 4.5 to 1.5 μ in size, and borne in groups held together in a slimy matrix on the apices of short conidiophores. Reddy and Holbert (1924) believed the fungus to be an active pathogen capable of invading seedlings and progressing systemically throughout the vascular system of the plant. Artificial inoculations with pure cultures of the organism were successful in reproducing some of the symptoms associated with the disease under natural conditions. Harris (1936) was unable to confirm the findings of Reddy and Holbert. In only a small percentage of cases did he find *C. acremonium* associated with discolored vascular bundles. Histological examination indicated darkening of the bundles to be due to deposition of gumlike substances in cells and vessels. Discoloration of vascular bundles could be induced by withholding water from plants or by supplying an unbalanced nutrient solution. Under field conditions drought or phosphorus deficiency accentuated discoloration of vascular bundles. Some inbred lines consistently showed the presence of discolored vascular bundles regardless of treatment. Harris had little success in inducing symptoms in plants by inoculation with the fungus. He considered that *C. acremonium* was not a vigorous parasite, but rather a saprophyte that occasionally penetrated through wounds to the vascular system. Observations by the writer are in general agreement with the conclusions of Harris. In view of the conflicting data, a reinvestigation of the problem would seem to be in order.

REFERENCES

- ALBERTS, H. W. 1927. Effect of pericarp injury on moisture absorption, fungus attack, and vitality of corn. *J. Am. Soc. Agron.* **19**: 1021-1030.
- ALLEN, R. F. 1933. The spermatia of corn rust *Puccinia sorghi*. *Phytopathology* **23**: 923-925.
- ALLEN, R. F. 1934. A cytological study of heterothallism in *Puccinia sorghi*. *J. Agr. Research* **49**: 1047-1068.
- ALSTATT, G. E. 1945. A new disease of corn in the Rio Grande Valley. *Plant Disease Repr.* **29**: 533-534.
- ARK, P. A. 1940. Bacterial stalk rot of field corn caused by *Phytomonas lapsa*. (Abstract) *Phytopathology* **30**: 1.
- ARK, P. A. 1941. Persistence of *Phytomonas lapsa* on seed of field corn. *Plant Disease Repr.* **25**: 202.
- ASHBY, S. F. 1927. *Macrophomina phaseoli* (Maubl.) comb. nov. The pycnidial stage of *Rhizoctonia bataticola*. *Trans. Brit. Mycol. Soc.* **12**: 141-147.
- BAIN, D. C., and EDGERTON, C. W. 1943. The zonate leaf spot, a new disease of sorghum. *Phytopathology* **33**: 220-226.
- BOEWE, G. H. 1936. The relation of ear rot prevalence in Illinois corn fields to ear coverage by husks. *State of Illinois Natural History Survey Division, Contrib. Sec. Appl. Botany and Plant Pathology. Publ. No.* **273**.
- BOEWE, G. H. 1938. Diplodia ear rot in Illinois corn fields. *Trans. Illinois State Acad. Sci.* **31**: 92-93.

- BOEWE, G. H. 1953. Stewart's Disease prospects for 1953. *Plant Disease Repr.* **37**: 311-312.
- BOWMAN, D. H. 1946. Sporidial fusion in *Ustilago maydis*. *J. Agr. Research* **72**: 233-243.
- BRANDES, E. W. 1920. Mosaic disease of corn. *J. Agr. Research* **19**: 517-522.
- BRANSTETTER, B. B. 1927. Corn root studies. *Missouri Agr. Expt. Sta. Research Bull.* **113**.
- BRESSMAN, E. N., and BARSS, H. P. 1933. Experiments with head smut of corn in western Oregon. *Phytopathology* **23**: 396-403.
- BURNHAM, C. R., and CARTLEDGE, J. L. 1939. Linkage relations between smut resistance and semi-sterility in maize. *J. Am. Soc. Agron.* **31**: 924-933.
- CHILTON, St. J. P. 1940. Delayed reduction of the diploid nucleus in the promycelia of *Ustilago zeae*. *Phytopathology* **30**: 622-623.
- CHRISTENSEN, J. J. 1926. The relation of soil temperature and soil moisture to the development of head smut in sorghum. *Phytopathology* **16**: 353-357.
- CHRISTENSEN, J. J. 1929. Hybridization in *Ustilago zeae*. *Minnesota Agr. Expt. Sta. Tech. Bull.* **65**.
- CHRISTENSEN, J. J. 1931. Studies in the genetics of *Ustilago zeae*. *Phytopathol. Z.* **4**: 129-188.
- CHRISTENSEN, J. J., and JOHNSON, I. J. 1935. Field reaction of varieties and selfed lines of corn to different collections of *Ustilago zeae*. *J. Agr. Research* **50**: 47-57.
- CLAYTON, E. E. 1927. Diplodia ear rot of corn. *J. Agr. Research* **34**: 357-371.
- COFFMAN, F. A., TISDALE, W. H., and BRANDON, J. F. 1926. Observations on corn smut at Akron, Colorado. *J. Am. Soc. Agron.* **18**: 403-411.
- CUGINI, G., and TRAVERSO, G. B. 1902. La *Sclerospora macrospora* Sacc. parrasita della *Zea mays* L. *Staz. sper. agr. ital.* **35**: 46-49.
- CUMMINS, G. B. 1931. Heterothallism in corn rust and the effect of filtering pycnial exudate. *Phytopathology* **21**: 751-753.
- CUMMINS, G. B. 1941. Identity and distribution of three rusts of corn. *Phytopathology* **31**: 856-857.
- CURZI, M. 1929. A serious new disease of maize. *Rend. accad. Inazl. Lincei. Ser. 6a.* **10**: 306-308 (*Rev. Appl. Mycol.* **9**: 174).
- DAVIDSON, R. S. 1950. Helminthosporium seedling blights of corn. (Abstract) *Phytopathology* **40**: 6.
- DAVIS, G. N. 1936. Some factors influencing the infection and pathogenicity of *Ustilago zeae* (Beckm.) Unger on *Zea mays* L. *Iowa Agr. Expt. Sta. Research Bull.* **199**.
- DIACHUN, S. 1939. The effect of some soil factors on *Penicillium* injury of corn seedlings. *Phytopathology* **29**: 231-241.
- DICKSON, J. G. 1923. Influence of soil temperature and moistures on the development of seedling blight of wheat and corn caused by *Gibberella saubinetii*. *J. Agr. Research* **23**: 837-870.
- DRECHSLER, C. 1925. Leaf spot of maize caused by *Ophiobolus heterostrophus* n.sp. the the ascigerous stage of a *Helminthosporium* exhibiting bipolar germination. *J. Agr. Research* **31**: 701-726.
- DRECHSLER, C. 1928. *Pythium arrhenomanes* n.sp. a parasite causing maize root rot. *Phytopathology* **18**: 873-875.
- DRECHSLER, C. 1934a. *Pythium butleri* and *P. aphanidermatum*. (Abstract) *Phytopathology* **24**: 7.
- DRECHSLER, C. 1934b. Phytopathological and taxonomic aspects of *Ophiobolus*, *Pyrenophora*, *Helminthosporium* and a new genus, *Cochliobolus*. *Phytopathology* **24**: 953-983.

- DURRELL, L. W. 1920. A preliminary study of purple sheath spot of corn. *Phytopathology* **10**: 487-495.
- DURRELL, L. W. 1923. Dry rot of corn. *Iowa Agr. Expt. Sta. Research Bull.* **77**.
- DURRELL, L. W. 1925. Basisporium dry rot of corn. *Iowa Agr. Expt. Sta. Research Bull.* **84**.
- EDDINS, A. H. 1930a. Dry rot of corn caused by *Diplodia macrospora*. *Phytopathology* **20**: 439-448.
- EDDINS, A. H. 1930b. A new diplodia ear rot of corn. *Phytopathology* **20**: 733-742.
- EDDINS, A. H. 1933. Infection of corn plants by *Physoderma zae-maydis* Shaw. *J. Agr. Research* **46**: 241-253.
- EDDINS, A. H., and VOORHEES, R. K. 1933. *Physalospora zicola* on corn and its taxonomic and host relationships. *Phytopathology* **23**: 63-72.
- EDWARDS, E. T. 1935. Studies on *Gibberella fujikuroi* var. *subglutinans*, the hitherto undescribed ascigerous stage of *Fusarium moniliforme* var. *subglutinans* and its pathogenicity on maize in New South Wales. *N. S. Wales, Dept. Agr. Sci. Bull.* **49**.
- ELLIOTT, C. 1941. Bacterial wilt of corn. *U. S. Dept. Agr. Farmers' Bull.* **1878**.
- ELLIOTT, C. 1942. Relative susceptibility to pythium root rot of twelve dent corn inbreds. *J. Agr. Research* **64**: 711-723.
- ELLIOTT, C. 1943. Pythium stalk rot of corn. *J. Agr. Research* **66**: 21-39.
- ELLIOTT, C., and JENKINS, M. T. 1946. *Helminthosporium turcicum* leaf blight of corn. *Phytopathology* **36**: 660-666.
- ELLIOTT, C., and POOS, F. W. 1934. Overwintering of *Aplanobacter stewarti*. *Science* [N. S.] **80**: 289-290.
- ELLIOTT, C., and POOS, F. W. 1940. Seasonal development, insect vectors, and host range of bacterial wilt of sweet corn. *J. Agr. Research* **60**: 645-686.
- ELLIS, J. B., and EVERHART, B. M. 1890. New North American fungi. *Proc. Nat'l Acad. Sci. Philadelphia* **42**: 219-249.
- FRAZIER, N. W. 1945. A streak disease of corn in California. *Plant Disease Repr.* **29**: 212-213.
- GARBER, R. J., and QUISENBERRY, K. S. 1925. Breeding corn for resistance to smut (*Ustilago zae*). *J. Am. Soc. Agron.* **17**: 132-140.
- GARBER, R. J., and HOOVER, M. M. 1928. The relation of smut infection to yield in maize. *J. Am. Soc. Agron.* **20**: 735-746.
- HAENSELER, C. M. 1937. Correlation between winter temperatures and incidence of sweet corn wilt in New Jersey. *Plant Disease Repr.* **21**: 298-301.
- HAIGH, J. C. 1928. *Macrophomina phaseoli* (Mauhl.) Ashby. The pycnidial stage of *Rhizoctonia bataticola*. *Trop. Agr. (Ceylon)* **70**: 77-79.
- HARRIS, M. R. 1936. The relationship of *Cephalosporium acremonium* to the black-bundle disease of corn. *Phytopathology* **26**: 965-980.
- HAYES, H. K., STAKMAN, E. C., GRIFFEE, F., and CHRISTENSEN, J. J. 1924. Reactions of selfed lines of maize to *Ustilago zae*. *Phytopathology* **14**: 268-280.
- HAYES, H. K., JOHNSON, I. J., and STAKMAN, E. C. 1933. Reaction of maize seedlings to *Gibberella saubinetii*. *Phytopathology* **23**: 905-911.
- HO, W. C. 1944. Soil inhabiting fungi attacking the roots of maize. *Iowa Agr. Expt. Research Bull.* **332**.
- HOFFER, G. N., and CARR, R. H. 1923. Accumulation of aluminum and iron compounds in corn plants and its probable relation to root rots. *J. Agr. Research* **23**: 801-821.
- HOFFMASTER, D. E., McLAUGHLIN, J. H., RAY, W. W., and CHESTER, K. S. 1943. The problem of dry rot caused by *Macrophomina phaseoli* (Abstract) *Phytopathology* **33**: 1113-1114.

- HOLBERT, J. R., ELLIOTT, C., and KOEHLER, B. 1933. Bacterial leaf blight of dent corn. (Abstract) *Phytopathology* **23**: 15-16.
- HOLBERT, J. R., HOPPE, P. E., and SMITH, A. L. 1935. Some factors affecting infection with and spread of *Diplodia zeae* in the host tissue. *Phytopathology* **25**: 1113-1114.
- HOOKE, A. L. 1951. The corn embryo as a factor in resistance to *Pythium* during germination. (Abstract) *Phytopathology* **41**: 17.
- HOOVER, M. M. 1932. Inheritance studies of the reaction of selfed lines of maize to smut (*Ustilago zeae*). *West Virginia Agr. Expt. Sta. Bull.* **253**.
- HOPPE, P. E. 1929. Inheritance of resistance to seedling blight of corn caused by *Gibberella saubinetii*. (Abstract) *Phytopathology* **19**: 79-80.
- HOPPE, P. E. 1943. Relative prevalence and geographic distribution of various ear rot fungi in the 1942 corn crop. *Plant Disease Repr.* **27**: 199-202.
- HOPPE, P. E. 1949. Differences in *Pythium* injury to corn seedlings at high and low temperatures. *Phytopathology* **39**: 77-84.
- HOPPE, P. E. 1951. A new technique for incubating seed corn in cold soil for disease tests. (Abstract) *Phytopathology* **41**: 18.
- HOPPE, P. E. 1952. The paper doll technique for disease tests of seed corn in cold soils. (Abstract) *Phytopathology* **42**: 11.
- HOPPE, P. E., and MIDDLETON, J. T. 1950. Pathogenicity and occurrence in Wisconsin soils of *Pythium* species which cause seedling disease in corn. (Abstract) *Phytopathology* **40**: 13.
- HUTTIG, W. 1931. Über den einfluss der temperatur auf die keimung geschlecht-vertielung bei Brandpilzen. *Z. Botan.* **24**: 529-557.
- HYRE, R. A. 1943. *Cercospora zeae-maydis* on corn in eastern Tennessee and Kentucky. *Plant Disease Repr.* **27**: 553-554.
- IMMER, F. R. 1927. The inheritance of reaction to *Ustilago zeae* in maize. *Minnesota Agr. Expt. Sta. Tech. Bull.* **51**.
- IMMER, F. R., and CHRISTENSEN, J. J. 1928a. Influence of environmental factors on the seasonal prevalence of corn smut. *Phytopathology* **18**: 589-598.
- IMMER, F. R., and CHRISTENSEN, J. J. 1928b. Determination of losses due to smut infections in selfed lines of corn. *Phytopathology* **18**: 599-602.
- IMMER, F. R., and CHRISTENSEN, J. J. 1931. Further studies on the reaction of corn to smut and effect of smut on yield. *Phytopathology* **21**: 661-674.
- ISLEY, D. 1950. The cold test for corn. *Tiré à part Compt. rend. l'assoc. intern. essais semences* **16**. (No. 2), Copenhagen V.
- ITZEROTT, D. 1938. Über keimung und wachstum von *Ustilago zeae* (Beckm.) Unger mit besonderer Berücksichtigung der infektion. *Phytopathol. Z.* **1**: 155-180.
- IVANOFF, S. S. 1933. Stewart's wilt disease of corn, with emphasis on the life history of *Phytomonas stewarti* in relation to pathogenesis. *J. Agr. Research* **47**: 749-770.
- IVANOFF, S. S. 1935. Studies on the host range of *Phytomonas stewarti* and *P. vascularum*. *Phytopathology* **25**: 992-1002.
- IVANOFF, S. S. 1936. Resistance to bacterial wilt of open-pollinated varieties of sweet, dent and flint corn. *J. Agr. Research* **53**: 917-926.
- IVANOFF, S. S., and RIKER, A. J. 1936. Resistance to bacterial wilt of inbred strains and crosses of sweet corn. *J. Agr. Research* **53**: 937-954.
- IVANOFF, S. S., RIKER, A. J., and DETTWILER, H. A. 1938. Studies on the cultural characteristics, physiology and pathogenicity of strain types of *Phytomonas stewarti*. *J. Bacteriol.* **35**: 235-253.
- JENKINS, M. T., and ROBERT, A. L. 1952. Inheritance of resistance to leaf blight of corn caused by *Helminthosporium turcicum*. *Agron. J.* **44**: 136-140.

- JENKINS, M. T., ROBERT, A. L., and FINDLEY, W. R., JR. 1952. Inheritance of resistance to *Helminthosporium* leaf blight in populations of F_3 progenies. *Agron. J.* **44**: 438-442.
- JOHANN, H. 1935. Histology of the caryopsis of yellow dent corn, with reference to resistance and susceptibility to kernel rots. *J. Agr. Research* **51**: 855-883.
- JOHANN, H. 1939. Scolecospores in *Diplodia zeae*. *Phytopathology* **29**: 67-71.
- JOHANN, H., and DICKSON, A. D. 1945. A soluble substance in corn stalks that retards the growth of *Diplodia zeae* in culture. *J. Agr. Research* **71**: 89-110.
- JOHANN, H., DICKSON, J. G., and WINELAND, G. 1923. Relation of environment to infection of corn seedlings by *Diplodia zeae* (Schw.) Lev. (Abstract) *Phytopathology* **13**: 52-53.
- JOHANN, H., HOLBERT, J. R., and DICKSON, J. G. 1928. A pythium seedling blight and root rot of dent corn. *J. Agr. Research* **37**: 443-464.
- JOHANN, H., HOLBERT, J. R., and DICKSON, J. G. 1931. Further studies on *Penicillium* injury to corn. *J. Agr. Research* **43**: 757-790.
- JOHNSON, I. J., and CHRISTENSEN, J. J. 1935. The relation between number, size and location of smut infections to reductions in yield of corn. *Phytopathology* **25**: 223-233.
- JOHNSON, A. G., CASH, L., and GARDNER, W. A. 1929. Preliminary report on a bacterial disease of corn. (Abstract) *Phytopathology* **19**: 81-82.
- JOHNSON, A. G., ROBERT, A. L., and CASH, L. 1945. Further studies on bacterial leaf blight and stalk rot of corn. (Abstract) *Phytopathology* **35**: 486-487.
- JOHNSON, A. G., ROBERT, A. L., and CASH, L. 1949. Bacterial leaf blight and stalk rot of corn. *J. Agr. Research* **78**: 719-732.
- JONES, D. F. 1918. Segregation of susceptibility to parasitism in maize. *Am. J. Botany* **5**: 295-300.
- JONES, E. S. 1923. Influence of temperature on the spore germination of *Ustilago zeae*. *J. Agr. Research* **24**: 593-597.
- JORGENSEN, L. R. 1929. Effect of smut infection on the yield of selfed lines and F_1 crosses in maize. *J. Am. Soc. Agron.* **21**: 1109-1112.
- KELMAN, A., and HERBERT, T. T. 1952. Evaluation of techniques for inoculating corn with *Physoderma zeae-maydis*. (Abstract) *Phytopathology* **42**: 284.
- KENDRICK, J. B. 1926. Holcus bacterial spot of *Zea mays* and *Holcus* species. *Iowa Agr. Expt. Sta. Research Bull.* **100**.
- KERNKAMP, M. F., and PETTY, M. A. 1941. Variation in the germination of chlamydospores of *Ustilago zeae*. *Phytopathology* **31**: 333-340.
- KOEHLER, B. 1935. Pathological significance of seed-coat injury in dent corn. (Abstract) *Phytopathology* **25**: 24.
- KOEHLER, B. 1939. Crazy top of corn. *Phytopathology* **29**: 817-820.
- KOEHLER, B. 1950. Improved techniques in hybrid seed corn production. Part II. Stalk and ear rot. *5th Ann. Hybrid Corn Industry-Research Conf.*
- KOEHLER, B. 1951. Husk coverage and ear declination in relation to corn ear rots. (Abstract) *Phytopathology* **41**: 22.
- KOEHLER, B. 1953. Ratings of some yellow corn inbreds for ear rot resistance. *Plant Disease Repr.* **37**: 440-444.
- KOEHLER, B., DUNGAN, G. H., and BURLISON, W. L. 1934. Maturity of seed in relation to yielding ability and disease infection. *J. Am. Soc. Agron.* **26**: 262-274.
- KOEHLER, B., and HOLBERT, J. R. 1930. Corn diseases in Illinois, their extent, nature and control. *Illinois Agr. Expt. Sta. Bull.* **354**.
- KOEHLER, B., and WOODWORTH, C. M. 1938. Corn seedling virescence caused by *Aspergillus flavus* and *A. tamarii*. *Phytopathology* **28**: 811-823.

- KORNFELD, A. 1937. Bekämpfung des Maisbeulenbrandes auf biologischer Grundlage. *Pflanzenkrankh.* **47**: 277–297.
- KUNKEL, L. O. 1927. The corn mosaic of Hawaii distinct from sugar cane mosaic. (Abstract) *Phytopathology* **17**: 41.
- KUNKEL, L. O. 1946. Leafhopper transmission of corn stunt. *Proc. Natl. Acad. Sci. U. S.* **32**: 246–247.
- KUNKEL, L. O. 1948. Studies on a new corn virus disease. *Arch. ges. Virusforsch. Band IV, Heft 1*, 24–46.
- KYLE, C. H. 1929. Relation of husk covering to smut of corn ears. *U. S. Dept. Agr. Tech. Bull.* **120**.
- KYLE, C. H. 1930. Relation between vigor of the corn plant and its susceptibility to smut (*Ustilago zae*). *J. Agr. Research* **41**: 221–231.
- LEFEBVRE, C. L., and SHERWIN, H. S. 1945. Races of *Helminthosporium turcicum*. (Abstract) *Phytopathology* **35**: 487.
- LENG, E. R. 1949. Differential reaction to penicillium seedling disease of corn. *Agron. J.* **41**: 435–439.
- LEONIAN, L. H. 1932. The pathogenicity and the variability of *Fusarium moniliforme* from corn. *West Virginia Agr. Expt. Sta. Bull.* **248**.
- LIMBER, D. P. 1927. *Fusarium moniliforme* in relation to diseases of corn. *Ohio J. Sci.* **27**: 232–246.
- LINCOLN, R. E. 1940. Bacterial wilt resistance and genetic host-parasite interactions in maize. *J. Agr. Research* **60**: 217–240.
- LIVINGSTON, J. E. 1945. Charcoal rot of corn and sorghum. *Nebraska Agr. Expt. Sta. Research Bull.* **136**.
- LUDBROOK, W. V. 1942. Top rot of maize, sweet corn, and sorghum. *J. Council Sci. Ind. Research* **15**: 213–219.
- MACKIE, W. W. 1932. A hitherto unreported disease of maize and beans. *Phytopathology* **22**: 637–644.
- MAGEE, J. A. 1948. Histological structure of the stem of *Zea mays* in relation to stiffness of stalk. *Iowa State Coll. J. Sci.* **22**: 257–268.
- MAINS, E. B. 1926. Studies in rust resistance. *J. Heredity* **17**: 313–325.
- MAINS, E. B. 1931. Inheritance of resistance to rust, *Puccinia sorghi*, in maize. *J. Agr. Research* **43**: 419–430.
- MAINS, E. B. 1938. Two unusual rusts of grasses. *Mycologia* **30**: 42–45.
- MAINS, E. B., TROST, F. J., and SMITH, G. M. 1924. Corn resistant to rust, *Puccinia sorghi*. (Abstract) *Phytopathology* **14**: 47.
- MCINDOE, K. G. 1931. The inheritance of reaction of maize to *Gibberella saubinetii*. *Phytopathology* **21**: 615–639.
- MCKEEN, W. E. 1951a. Seedling susceptibility of dent corn inbreds to root rot caused by *Pythium arrhenomanes*. *Sci. Agr.* **31**: 475–479.
- MCKEEN, W. E. 1951b. A preliminary study of corn seedling blight in southern Ontario. *Can. J. Botany* **29**: 125–137.
- MCKEEN, W. E. 1951c. An exceptionally early outbreak of corn rust in Canada. *Plant Disease Repr.* **35**: 367.
- MCNEW, G. L. 1937a. Crown infection of corn caused by *Diplodia zae*. *Iowa Agr. Expt. Sta. Research Bull.* **216**.
- MCNEW, G. L. 1937b. Isolation of variants from cultures of *Phytomonas stewartii*. *Phytopathology* **27**: 1161–1170.
- MCNEW, G. L. 1938. The relation of nitrogen nutrition to virulence in *Phytomonas stewartii*. *Phytopathology* **28**: 769–786.

- McNEW, G. L. 1940a. Invasion of sweet corn plants of different ages by strains of *Phytomonas stewarti*. *Phytopathology* **30**: 244-249.
- McNEW, G. L. 1940b. Factors influencing attenuation of *Phytomonas stewarti* cultures. *J. Bacteriol.* **39**: 171-186.
- MELHUS, I. E., VAN HALTERN, F. H., and BLISS, D. E. 1928. A study of *Sclerospora graminicola* on *Setaria viridis* and *Zea mays*. *Iowa Agr. Expt. Sta. Research Bull.* **111**.
- MENZIES, J. D., and STANBERRY, C. O. 1947. The effect of terminal smut galls on yield and seed grade of detasseled hybrid corn. (Abstract) *Phytopathology* **37**: 363.
- MIDDLETON, J. T. 1943. The taxonomy, host range and geographical distribution of the genus *Pythium*. *Mem. Torrey Botan. Club* **20** (No. 1): 1-171.
- MITCHELL, H. H., and BEADLES, J. R. 1940. The impairment in nutritive value of corn grain damaged by specific fungi. *J. Agr. Research* **61**: 135-142.
- NATTRASS, R. M. 1953. Occurrence of *Puccinia polysora* in East Africa. *Nature* **171**: 527.
- NIEDERHAUSER, J. S., and CERVANTES, J. 1950. Transmission of corn stunt in Mexico by a new insect vector, *Baldulus elimatus*. (Abstract) *Phytopathology* **40**: 20.
- NISIKADO, Y., and MIYAKE, C. 1926. Studies on two Helminthosporium diseases of maize caused by *Helminthosporium turcicum* Pass. and *Ophiobolus heterostrophus* Drechs. *Helminthosporium maydis* Niskado et Miyake. *Ber. Ohara Inst. landwirtsch. Forsch. Kurashiki, Japan Band III* (Heft 2): 221-266.
- OJERHOLM, E. 1934. Multiciliate zoospores in *Physoderma zae-maydis*. *Bull. Torrey Botan. Club* **61**: 13-18.
- PADY, S. N. 1943. Diseases of corn in Northeastern Kansas. *Plant Disease Repr.* **27**: 338.
- PATE, J. B. 1950. Studies on *Helminthosporium maydis* and *H. carbonum* leaf diseases of corn. (Abstract) *Phytopathology* **40**: 790.
- PEGLION, V. 1930. La formazione dei conidi e la germinazione delle oospore della *Sclerospora macrospora* Sacc. *Boll. staz. patol. vegetale* [N. S.] **10**: 153-164 (*Rev. Appl. Mycol.* **10**: 174).
- PEPPER, B. B., and HAENSELER, C. M. 1944. Control of European corn borer and ear smut on sweet corn with dusts and sprays. *New Jersey Agr. Expt. Sta. Circ.* **486**.
- PEYRONEL, B. 1929. Gli zoosporangi nella *Sclerospora macrospora*. *Boll. staz. patol. vegetale* [N. S.] **9** (4), 353-357.
- PICKETT, B. S., GODFREY, G. H., ALTSTATT, G. E., MELHUS, I. E., and WALLIN, J. R. 1946. A disease of corn in the Rio Grande Valley in Texas. *Iowa State Coll. J. Sci.* **20**: 423-428.
- PIEMEISEL, F. J. 1917. Factors affecting parasitism of *Ustilago zae*. *Phytopathology* **7**: 294-307.
- PLATZ, G. A. 1929. Some factors influencing the pathogenicity of *Ustilago zae* (Beckm.) Unger. *Iowa State Coll. J. Sci.* **3**: 177-214.
- PONTIS-VIDELA, R. E. 1951. Una podreumbre del tallo del maiz (*Zea mays* L.) en Venezuela causada por *Pythium aphanidermatum*. *Agronomia Tropical Maracay* **1**: 13-28.
- POOS, F. W., and ELLIOTT, C. 1936. Certain insect vectors of *Aplanobacter stewarti*. *J. Agr. Research* **52**: 585-608.
- POTTER, A. A. 1914. Head smut of sorghum and maize. *J. Agr. Research* **2**: 339-371.
- POTTER, A. A., and MELCHERS, L. E. 1925. Study of the life history and ecologic relationships of the smut of corn. *J. Agr. Research* **30**: 161-173.
- RALEIGH, W. P. 1930. Infection studies of *Diplodia zae* and control of seedling blights in corn. *Iowa Agr. Expt. Sta. Research Bull.* **124**.

- RAND, F. V., and CASH, L. C. 1924. Further evidence of insect dissemination of bacterial wilt of corn. *Science* [N. S.] **59**: 67-69.
- RANDS, R. D., and DOPP, E. 1934. Variability in *Pythium arrhenomanes* to root rot of sugar cane and corn. *J. Agr. Research* **49**: 189-221.
- REDDY, C. S. 1933. Resistance of dent corn to *Basisporium gallarum* Moll. *Iowa Agr. Expt. Sta. Research Bull.* **167**.
- REDDY, C. S., and HOLBERT, J. R. 1924. The black-bundle disease of corn. *J. Agr. Research* **27**: 177-205.
- REED, G. M., SWABLY, M., and KOLK, L. 1927. Experimental studies on head smut of corn and sorghum. *Bull. Torrey Botan. Club* **54**: 295-310.
- RHIND, D., WATERSTON, J. M., and DEIGHTON, F. C. 1952. Occurrence of *Puccinia polysora* in West Africa. *Nature* **169**: 631.
- RHOADES, V. H. 1935. The location of a gene for disease resistance in maize. *Proc. Nat. Acad. Sci.* **21**: 243-246.
- ROANE, C. W. 1950. Observations on corn diseases in Virginia from 1947 to 1950. *Plant Disease Repr.* **34**: 394-396.
- ROBERT, A. L. 1952. Cultural and pathogenic variability in single-conidial and hyphal-tip isolates of *Helminthosporium turcicum* Pass. *U. S. Dept. Agr. Tech. Bull.* **1058**.
- ROBERT, A. L., and FINDLEY, W. R., JR. 1952. Diseased corn leaves as a source of infection in artificial and natural epidemics of *H. turcicum*. *Plant Disease Repr.* **36**: 9-10.
- ROSEN, H. R. 1922a. The bacterial pathogen of corn stalk rot. *Phytopathology* **12**: 497-498.
- ROSEN, H. R. 1922b. A bacterial disease of foxtail. *Ann. Missouri Botan. Garden* **9**: 333-402.
- RUSH, G. E., and NEAL, N. P. 1951. The effect of maturity and other factors on stands of corn at low temperatures. *Agron. J.* **43**: 112-116.
- SABOE, L. C., and HAYES, H. K. 1941. Genetic studies of reaction to smut and of firing in maize by means of chromosomal translocations. *J. Am. Soc. Agron.* **33**: 463-470.
- SCURTI, I. 1949. Anzione a distanza del micelio nelle neoformazioni da *Ustilago maydis*. *Nuovo G. Bot. Ital.* [N. S.] **56**: 740-741 (*Rev. Appl. Mycol.* **30**: 34, 1951).
- SCURTI, I. 1950. Sulla istopatologia del mais parassitato dall' *Ustilago maydis*. *Ann. sper. agrar. Rome* [N. S.] **4**: 827-855 (*Rev. Appl. Mycol.* **30**: 152, 1951).
- SEMENIUK, G. 1942. Charcoal rot of maize, new to Iowa. (Abstract) *Proc. Iowa Acad. Sci.* **49**: 256.
- SEMENIUK, G. 1944. Seedling infection of dent maize by *Sclerotium bataticola*. *Phytopathology* **34**: 838-843.
- SLAGG, C. M. 1944. Diseases of corn in Nebraska and Kansas. *Plant Disease Repr.* **28**: 1041-1042.
- SLEUMER, H. O. 1932. Uber sexualitat und zytologie von *Ustilago zae* (Beckm.) Unger. *Z. Botan.* **25**: 209-263.
- SMITH, F. L. 1936. The effect of corn smut on the yield of grain in the San Joaquin Valley of California. *J. Am. Soc. Agron.* **28**: 257-265.
- SMITH, F. L., and MADSEN, C. B. 1949. Susceptibility of inbred lines of corn to fusarium ear rot. *Agron. J.* **41**: 347-348.
- SMITH, G. M. 1933. Golden Cross Bantam Sweet Corn. *U. S. Dept. Agr. Circ.* **268**.
- SMITH, M. A. 1926. Infection and spore germination studies with *Puccinia sorghi*. (Abstract) *Phytopathology* **16**: 69.
- SPARROW, F. K. 1934. The occurrence of true sporangia in the Physoderma disease of corn. *Science* [N. S.] **79**: 563-564.

- SPENCER, E. L., and McNEW, G. L. 1938. The influence of mineral nutrition on the reaction of sweet corn seedlings to *Phytophthora Stewarti*. *Phytopathology* **28**: 213-223.
- STAKMAN, E. C., CHRISTENSEN, J. J., and BREWBAKER, H. E. 1928. Physiologic specialization in *Puccinia sorghi*. *Phytopathology* **18**: 345-354.
- STAKMAN, E. C., TYLER, L. J., and HAFSTAD, G. E. 1933. The constancy of cultural characters and pathogenicity in variant lines of *Ustilago zeae*. *Bull. Torrey Botan. Club* **60**: 565-572.
- STANDEN, J. H. 1939. The prevalence of *Basisporium gallarum* in arrested axillary shoots and secondary ears of maize. *Phytopathology* **29**: 656-657.
- STANDEN, J. H. 1944. Chemical and physical characteristics of maize cobs in relation to the growth of *Nigrospora oryzae*. *Phytopathology* **34**: 315-323.
- STANDEN, J. H. 1945. *Nigrospora oryzae* (B. and Br.) Petch on maize. *Phytopathology* **35**: 552-564.
- STANLEY, A. R., and ORTON, C. R. 1932. Bacterial stalk rot of sweet corn. (Abstract) *Phytopathology* **22**: 26.
- STEVENS, N. E. 1934. Stewart's disease in relation to winter temperatures. *Plant Disease Repr.* **18**: 141-149.
- STEVENS, N. E. 1936. Second experimental forecast of the incidence of bacterial wilt of corn. *Plant Disease Repr.* **20**: 109-113.
- STEVENS, N. E., and HAENSELER, C. M. 1940. Sixth experimental forecast of the incidence of bacterial wilt on sweet corn. *Plant Disease Repr.* **24**: 122-129.
- STEVENS, N. E., and HAENSELER, C. M. 1941. Incidence of bacterial wilt of sweet corn, 1935-1940: forecast and performance. *Plant Disease Repr.* **25**: 152-157.
- STEVENS, N. E., and WOOD, J. I. 1935. Losses from corn ear rots in the United States. *Phytopathology* **25**: 281-283.
- STEWART, F. C. 1897. A bacterial disease of sweet corn. *New York (Geneva) Agr. Expt. Sta. Bull.* **130**.
- STONEBERG, H. F. 1927. The productiveness of corn as influenced by the mosaic disease. *U. S. Dept. Agr. Tech. Bull.* **10**.
- STONER, W. N. 1950. A preliminary report of results from some fungicidal spray trials for control of *Helminthosporium* leaf blight of sweet corn. *Plant Disease Repr.* **34**: 312-313.
- STONER, W. N. 1951. A report on the influence of spray additives on control of *Helminthosporium turcicum* in the Everglades. *Plant Disease Repr.* **35**: 487-488.
- STONER, W. N. 1952. Leaf fleck, an aphid borne persistent virus disease of maize. *Phytopathology* **42**: 683-689.
- STOUT, G. L. 1930. New fungi found on the Indian Corn plant in Illinois. *Mycologia* **22**: 271-287.
- STOVER, W. G. 1922. The relation of soil temperature to the development of the seedling blight of corn caused by *Helminthosporium* sp. (Abstract) *Phytopathology* **12**: 30.
- STRINGFIELD, G. H., and BOWMAN, D. H. 1942. Breeding corn hybrids for smut resistance. *J. Am. Soc. Agron.* **34**: 486-494.
- TATUM, L. A., and ZUBER, M. S. 1943. Germination of maize under adverse conditions. *J. Am. Soc. Agron.* **35**: 48-59.
- TEHON, L. R., and BOEWE, G. H. 1939. Charcoal rot in Illinois. *Plant Disease Repr.* **23**: 312-325.
- TEHON, L. R., and DANIELS, E. Y. 1925. Notes on the parasitic fungi of Illinois II. *Mycologia* **17**: 240-249.

- TEHON, L. R., and DANIELS, E. Y. 1927. Notes on the parasitic fungi of Illinois III. *Mycologia* **19**: 110-129.
- THIRUMALACHAR, M. J., SHAW, C. G., and NARASIMHAN, M. J. 1953. The sporangial phase of the downy mildew on *Eleusine coracana* with a discussion of the identity of *Sclerospora macrospora*. *Bull. Torrey Botan. Club* **80**: 299-307.
- TISDALE, W. H. 1919. Physoderma disease of corn. *J. Agr. Research* **16**: 137-154.
- TOWNSEND, G. R. 1951. Control of the leaf blight and rust diseases of sweet corn. *Plant Disease Reprtr.* **35**: 368-369.
- ULLSTRUP, A. J. 1944. Further studies on a species of *Helminthosporium* parasitizing corn. *Phytopathology* **34**: 214-222.
- ULLSTRUP, A. J. 1946. An undescribed ear rot of corn caused by *Physalospora zeae*. *Phytopathology* **36**: 201-212.
- ULLSTRUP, A. J. 1949. A method for producing artificial epidemics of diplodia ear rot. *Phytopathology* **39**: 93-101.
- ULLSTRUP, A. J. 1951. The effect of some leaf diseases on grain yields in corn. (Abstract) *Phytopathology* **41**: 36.
- ULLSTRUP, A. J. 1952. Observations on crazy top of corn. *Phytopathology* **42**: 675-680.
- ULLSTRUP, A. J., and BRUNSON, A. M. 1947. Linkage relationships of a gene in corn determining susceptibility to a *Helminthosporium* leaf spot. *J. Am. Soc. Agron.* **39**: 606-609.
- VALLEAU, W. D. 1920. Seed corn infection with *Fusarium moniliforme* and its relation to root and stalk rots. *Kentucky Agr. Expt. Sta. Bull.* **226**.
- VALLEAU, W. D., KARRAKER, P. E., and JOHNSON, E. M. 1926. Corn root rot, a soil-borne disease. *J. Agr. Research* **33**: 453-476.
- VOORHEES, R. K. 1933a. *Gibberella moniliformis* on corn. *Phytopathology* **23**: 368-378.
- VOORHEES, R. K. 1933b. Effect of certain environmental factors on the germination of the sporangia of *Physoderma zeae-maydis*. *J. Agr. Research* **47**: 609-615.
- VOORHEES, R. K. 1934. Sclerotial rot of corn caused by *Rhizoctonia zeae*. *Phytopathology* **24**: 1290-1303.
- WALLIN, J. R. 1951. An epiphytotic of corn rust in the north central region of the United States. *Plant Disease Reprtr.* **35**: 207-211.
- WALTER, J. M. 1934. The mode of entrance of *Ustilago zeae* into corn. *Phytopathology* **24**: 1012-1020.
- WEBER, G. F. 1922. Studies on corn rust. *Phytopathology* **12**: 89-97.
- WELLHAUSEN, E. J. 1937a. Effect of the genetic constitution of the host on the virulence of *Phytomonas stewarti*. *Phytopathology* **27**: 1070-1089.
- WELLHAUSEN, E. J. 1937b. Genetics of resistance to bacterial wilt in maize. *Iowa Agr. Expt. Sta. Research Bull.* **224**.
- WELLMAN, F. L. 1934. Infection of *Zea mays* and various other *Gramineae* by the celery virus in Florida. *Phytopathology* **24**: 1035-1037.
- WERNHAM, C. C. 1951. Cold testing corn, a chronological and critical review. *Penn. State Coll. Progr. Reprt. No.* **47**.
- WESTON, W. H., JR. 1929. The occurrence of *Sclerospora graminicola* on maize in Wisconsin. *Phytopathology* **19**: 391-397.
- YOUNG, G. Y., LEFEBVRE, C. L., and JOHNSON, A. G. 1947. *Helminthosporium rostratum* on corn, sorghum and pearl millet. *Phytopathology* **37**: 180-183.

CHAPTER XIII

The Most Important Corn Insects

F. F. DICKE

I. Introduction

In a broad sense a particular crop is part of an agricultural system. A major crop such as corn, with its many phases of production and utilization under widely different environmental conditions, presents many interrelated problems in which insects are commonly involved.

In one way or another corn is subject to insect attack from the time it is planted until it is consumed as food or feed. Other crops, particularly small grains, forage grasses, and legumes, frequently are sources of insects that attack corn and must be considered as a part of the corn-insect problem.

The objective of this section is to present the more significant information on the insects that are most troublesome on the corn crop in the field and in storage. It has been customary to classify the injurious species according to their habitat or to the plant structures that they commonly infest. The stage of plant development is frequently an important factor in determining what structures are attacked and in the food habits and damage potential of the insects attacking them. The species have therefore been classified broadly as follows: (1) soil insects, (2) insects attacking leaf, stalk, and ear, (3) insects in relation to diseases of corn, and (4) stored-grain insects. It is beyond the scope of this section to give descriptions of characters used by taxonomists for making specific identifications. Such identifications are encouraged; ordinarily, however, descriptions of the injurious forms and their typical injury are ample for tentative general field determinations.

An attempt has been made to cite publications that include good bibliographies. Many of the early records on distribution, abundance, and biology of corn insects that are not cited were assembled by the United States Entomological Commission or the Division of Entomology of the Department of Agriculture and by the state entomologists of the several states, especially New York, Illinois, and Missouri. The most complete special reports on corn insects are those of Forbes (1893, 1905) in Illinois.

A survey of the literature on the insects that have been recorded on corn reveals a rather large number of species. Many of them do not have a proved food host relationship or are of minor importance. In discussing the sources of American corn insects, Neiswander (1926) listed slightly fewer than 400 species. Since his publication there has been little change in the general corn-insect complex with respect to the injurious species. However, changes in agricultural and marketing practices and in standards for farm products, including corn, have brought about a shift in the relative status of some of the species within the complex. With increased emphasis on stricter grading and product purity, more vigilance is required in the application of measures to prevent insect damage or contamination.

II. Research Trend

Records of the identity, prevalence, and biology of corn insects in America prior to the establishment of official entomology in 1854 are scattered and somewhat fragmentary. However, information from various sources shows that the complex before the days of systematic records was similar to what it is today. The major groups infesting different parts of the plant and the grain were well represented. Some species have been added to these groups through introduction from foreign sources.

The epizootics of many of the important species show a periodicity pattern, although not necessarily in regular cycles. Populations may remain relatively stable for several years and then suddenly increase. The limiting factors in such periodicity are climatic and biological in nature. A high rate of survival in some insects is favored by dry and warm conditions during critical periods of development and activity; other species are favored by cool moist conditions. The variable pattern of the environment therefore affects the general corn-insect complex from year to year.

Much of the research to develop measures to control corn insects has centered around applied biological and ecological methods. A good deal of emphasis has been placed on natural enemies, and efforts have been directed toward methods of limiting populations through adjustments in plowing and planting time, crop rotation, sanitation, and barriers. The effect of compatible cultural practices in reducing insect abundance in corn is perhaps of greater significance than is commonly appreciated. Through usage many such practices have become established procedure. Others, such as indiscriminate burning and fall plowing to destroy overwintering forms, have gone into discard with the adoption of better agronomic and soil-conservation methods.

The last two decades have seen a general turnover from open-pollinated to hybrid varieties of corn. Significantly better in yields and standing ability and in tolerance to insects and diseases, hybrid corn has had a considerable impact on various aspects of research on corn insects. The development of inbred lines and hybrids that are either tolerant or resistant to ear worms, rootworms, stalk borers, and even to field infestations of insects that are principally pests of the stored grain, is receiving increased attention in many breeding programs.

The introduction and use of more efficient insecticides and the development of better equipment for applying them have also been important factors in the improved control of corn insects. The development of the chlorinated hydrocarbon and organic phosphorus toxicants and methods of applying them have been phenomenal during the last decade. Concurrently a great deal of effort has been devoted to investigating the various aspects of residues and the safeguards required in the use of the new insecticides. As a result insecticidal control for some of the dominant corn insects can be expected to become even more practical and efficient and come into more widespread use.

III. Soil Insects

Soil insects are those that inhabit the soil while they are in some way causing plant injury. The soil forms may be injurious to the roots or other subterranean parts of the plant, or, as is the case with cutworms and some beetles, they may sever or feed on plant parts above the ground. Because they are hidden in the soil, many of these insects ordinarily escape attention when in the immature form but may be well known in the adult stage. Plant injury above ground is commonly the first indication of an infestation. However, with a knowledge of their adaptations and habits one can usually detect where certain species are apt to be most abundant. The species of soil insects from an economic standpoint have been treated more in groups than those feeding on the aerial parts of the plant, perhaps because of the large number of species involved. Thus, cutworms, wireworms, and white grubs have been grouped, although there may be deviations in biology among the species within a group.

1. Corn Rootworm (*Diabrotica longicornis* (Say))

a. Description, Injury, and Distribution. The larvae of the corn rootworm (also called the northern rootworm) are slender, white to pale-yellow, with yellowish-brown heads, and about $\frac{3}{10}$ inch long when full grown. The young larvae consistently invade the young lateral

roots, causing them to turn reddish or brown. Later stages commonly injure the young lateral root buds near the base of the stalk. The pupae are naked and white, and located in earthen cells in the soil near the base of the plant. The adults are about $\frac{1}{5}$ inch long and pale-green, and during the latter part of the summer are injurious on the silks and tips of ears of corn and on the flowers of other plants. The larva, pupa, and adult are illustrated in Fig. 1. The species is predominantly a pest in the central states, but also occurs in the eastern and southern states (Forbes, 1893; Webster, 1913b).

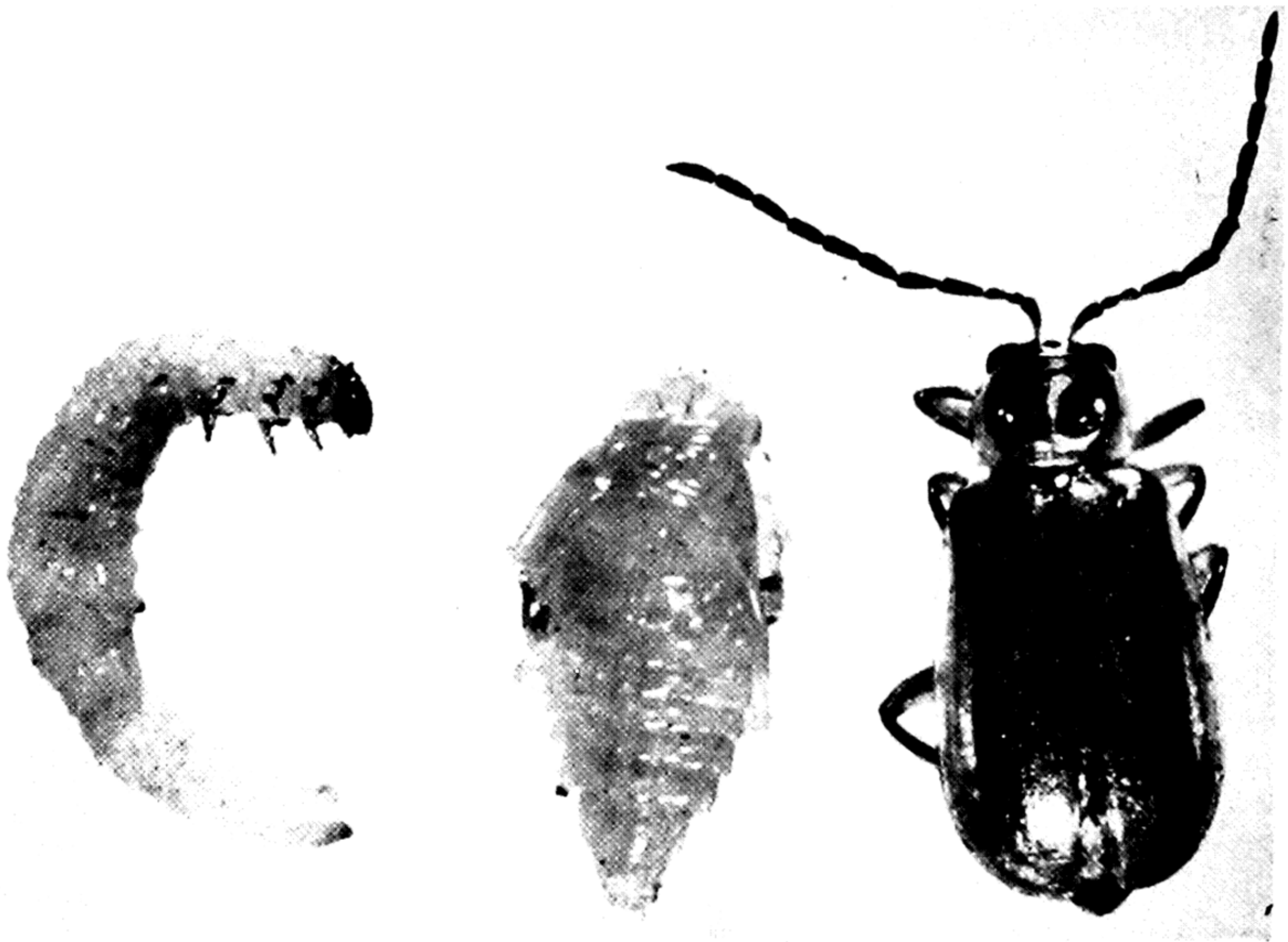


FIG. 1. Three stages in the life cycle of the corn rootworm. From left to right: larva; pupa; adult. (Courtesy of the Iowa Agricultural Experiment Station.)

b. Habits and Biology. The corn rootworm has a single generation annually. The adults emerge in the summer and are prevalent in corn fields until fall. They feed gregariously on the silks and also eat the pollen of corn and other plants. The eggs are deposited in the soil in corn and oat fields in the latter part of the summer. This habit is an important factor in the fate of the progeny the following year. When corn follows corn or a single intervening crop of oats, a favorable environment is provided for the development of the next generation. After hatching, late in the spring, the young larvae establish themselves in young roots or perish. Their feeding in the lateral roots results in poor root growth or "root pruning," as shown in Fig. 2, with varying de-



FIG. 2. Corn roots severely damaged by the corn rootworm. The lower brace roots have been completely denuded, allowing the entrance of root rot organisms. Development of brace roots occurred on the side next to the ground after the plant lodged. (Courtesy of Iowa Agricultural Experiment Station.)

degrees of regeneration of fibrous secondary roots. The invaded parts become reddish or brownish and are commonly infected with root rot, a condition that may be implicated in varietal response (Forbes, 1893; Bigger, 1932).

The more advanced larvae also feed on the rings of lateral root buds below the soil surface, interfering with lateral root development. Thus in a heavy infestation plants are poorly anchored and are very sus-

ceptible to root lodging, as illustrated in Fig. 3. Because of its interference with harvesting, lodging is perhaps as important in the rootworm problem as loss of yield. According to Tate and Bare (1946),



FIG. 3. Field of dent corn showing lodging and chaffy ears as a result of rootworm damage. (Courtesy of the Iowa Agricultural Experiment Station.)

continuous crops of corn and moist soil conditions favor the development and survival of larvae. The problem is most severe in Nebraska under irrigated conditions.

c. Varietal Resistance. The response to root injury by the corn rootworm in different inbred lines appears to be associated with the inherent ability of the plant to regenerate roots. In a test of 200 top crosses in Iowa in 1952 the parent lines 38-11, B2, and B14, or deriva-

tives of crosses involving these lines, regenerated their roots and had good lodging resistance under a high level of rootworm infestation.

d. Cultural Practices. The corn rootworm problem is associated with cropping practices. For many years rotation of crops, with not more than two successive crops of corn, has been advocated in time of threatening rootworm populations (Forbes, 1893). Bigger (1932) showed that a four-year rotation gave almost complete relief, whereas a short rotation using an intervening crop of oats and sweetclover did not adequately reduce rootworm injury—an indication that substantial egg deposition took place in oats-stubble ground.

Tate and Bare (1946), working in Nebraska, found less lodging after fall plowing, listed planting, and timely irrigation than after other cropping practices. Excessive irrigation at tasseling time and thereafter increased lodging. In further tests in Nebraska Hill *et al.* (1948) reported increased yields and reduction in lodging under irrigation when corn was grown in rotation with sweetclover, when it was fertilized with nitrogen, or when manure was applied. Nitrogen did not decrease rootworm populations but stimulated root recovery.

e. Chemical Control Measures. In connection with their experiments on cultural control practices, Hill *et al.* (1948) tested BHC at 1 or 2 pounds of the gamma isomer per acre as a surface treatment before plowing and at 0.8, 1.6, or 2.4 pounds per acre as a side dressing. Rootworm populations and lodging of the corn plants were greatly reduced with these treatments. DDT gave little better control than the checks. On dry land BHC decreased lodging but did not increase the yield significantly. More benefit was derived from cultural practices and fertilizer treatment than from insecticide applications.

In tests of several insecticides and methods of application, including fertilizer-insecticide combinations, Cox and Lilly (1953) obtained significant reductions in rootworm populations with aldrin, dieldrin, chlordane, heptachlor, and gamma BHC, in broadcast and band methods, but failed to obtain reductions by a deep-placement side dressing of a fertilizer-insecticide mixture. Aldrin was the most effective insecticide, but good results were also obtained with chlordane, dieldrin, heptachlor, and BHC. DDT was not satisfactory.

Diabrotica virgifera, a closely related species of rootworm on corn, frequently called the western or Colorado corn rootworm, has periodically been important in Colorado, Nebraska, and Kansas. This species has moved eastward and its distribution now overlaps with that of *D. longicornis*. The larvae are similar in appearance and habits to those of *D. longicornis*, and similar conditions favor their development and survival. The adults are greenish and are distinguished by a horizontal

stripe on the wings. The life history is practically the same as that of *D. longicornis* and the same control practices are advocated (Gillette, 1912; Tate and Bare, 1946).

2. *Southern Corn Rootworm* (*Diabrotica undecimpunctata howardi* (Barber))

a. Description, Injury, and Distribution. The southern corn rootworm, also known as the spotted cucumber beetle, injures corn in both

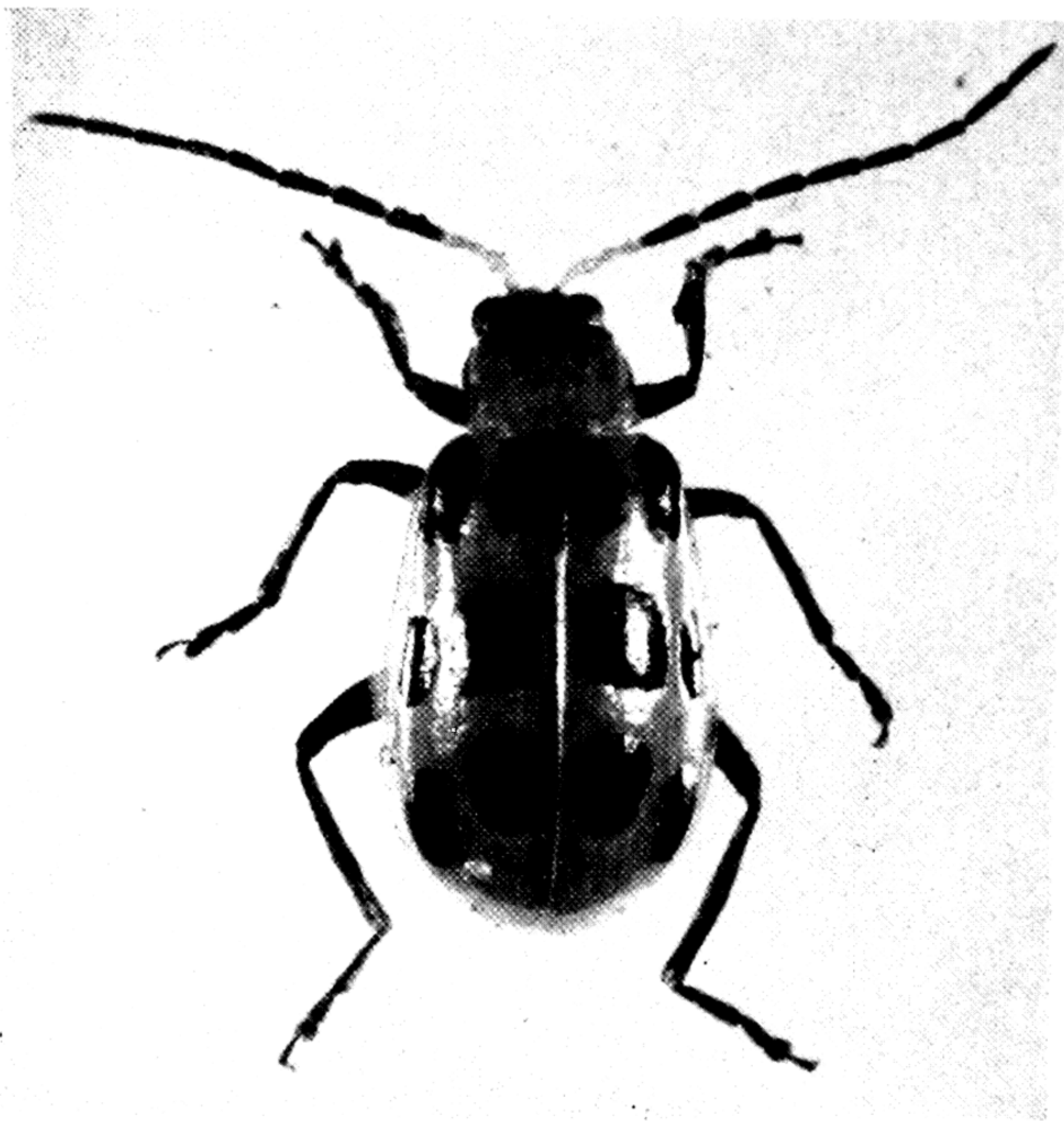


FIG. 4. Southern corn rootworm adult. (Courtesy of the Iowa Agricultural Experiment Station.)

the larval and the adult stages. The young larvae are slender, white to yellowish, becoming greenish-yellow as they mature. The full-grown larva is about $\frac{1}{2}$ inch long and has a brownish head shield and brown dorsal shield on the ninth abdominal segment. The larvae and pupae resemble those of the corn rootworm (Fig. 1) and are easily confused with them. The adult (Fig. 4) is about $\frac{1}{4}$ inch long, green, with 11 or 12 black spots on the wings. Symptoms of larval injury are holes through the base of small plants, tillering following growing point injury, and root injury similar to that described for the corn rootworm (Forbes, 1893; Webster, 1913a).

The southern corn rootworm has many hosts among the grasses, cucurbits, and legumes. It is widely distributed east of the Rocky Mountains, including southern Canada, but is most serious as a pest of corn in the southeastern states and in the lower and middle Mississippi Valley.

b. Habits and Biology. The southern corn rootworm overwinters as an adult under debris but may be active or feed on green plants on warm days in the winter in the deep South. In the spring the beetles fly to legumes, cucurbits, or grasses, where they feed and deposit their eggs in the soil. In southern areas, according to Isely (1929) and Arant (1929), the main source of the injury to young corn is from early-stage larvae that were present in the soil prior to seed-bed preparation and corn planting. However, oviposition has been observed after corn emergence. In areas where this species is a pest, cool and wet springs are favorable for building up populations in winter legumes and on low lands where favorable hosts are prevalent.

The first brood of larvae feed in or on the young roots and also burrow through the plants near the base. This feeding stunts or kills the growing point of plants and frequently induces tillering. Luginbill (1918) reported the first brood of larvae as the most important on corn in South Carolina. However, there appears to be an overlapping of generations, and Isely (1929) concluded that in Arkansas the number of generations was indeterminate. In the northern areas there are thought to be one or two generations. Forbes (1893) reported root pruning and subsequent root lodging after the bud-feeding stage and presence of larvae from June to August. On older corn larval feeding was found in the base of the stalk, on the young brace roots, and on the lower leaf sheaths.

The injury in the northern states is easily confounded with that of the corn rootworm, *Diabrotica longicornis*. In the southern areas the injury may be mistaken for that of *Diatraea* spp., the sugar-cane beetle, or wireworms. The adults commonly feed on the leaves of corn from the seedling to later whorl stages of growth and on the silks. The feeding on the bud leaves may be confused with that of some of the lepidopterous budworms.

c. Varietal Resistance. An important quality in inbred lines or in hybrids is a root system that will resist lodging. Some lines respond more than others to regeneration of roots after rootworm injury. In tests at the Ohio Agricultural Experiment Station the inbred Oh56 was much less damaged than Oh02 (Anonymous, 1937-1938). The superiority of Oh56 was attributed to stimulation of lateral root development when the primary roots were damaged. Bigger *et al.* (1938) reported

that tests in Illinois showed hybrids to be more resistant to this rootworm than open-pollinated varieties. Recovery of roots and resistance to root rots following attack were thought to be the important factors in resistance. Bigger *et al.* (1941) reported on the results of tests of both inbred lines and crosses. The inbred line 38-11 was outstanding in resistance to lodging following rootworm attack and transmitted this quality to crosses. Their data also indicated a differential response among inbred lines to adult attack.

d. Cultural Practices. Various cultural practices have been advocated for reducing rootworm injury, such as crop rotation, thick planting, fertilization, green manure crops, clean tillage, and adjustment of planting dates. Good soil and fertilization practices minimize the rootworm injury by stimulating root development. Isely (1929) recommended the elimination of wild grasses, on which the larval infestation begins, about a month before the planting of corn. Similarly Arant (1934) and Eden and Arant (1953) suggested turning under winter legumes on or before April 15 and planting early in May in areas with a climate similar to that in Alabama.

e. Chemical Control Measures. Chemical control measures for the southern corn rootworm are of recent development. Fulton (1946) obtained promising results with DDT and BHC. Floyd and Smith (1949) presented data showing the effect of fertilizer and insecticide-fertilizer combinations on stands. In their tests BHC (1 pound of the gamma isomer per acre) and chlordane (5 pounds per acre) were very effective in reducing rootworm injury. Eden and Arant (1953) report effective control with 1 pound of aldrin or dieldrin per acre mixed with a fertilizer and applied at planting time. They consider lindane seed treatments as promising.

3. Cutworms—Many Species

a. Description, Injury, and Distribution. Cutworms are the larvae of noctuid moths. The typical cutworm commonly found attacking corn has a plump curled-up appearance. The black cutworm is shown in Fig. 5. The color of the larvae varies with the species from a light-glassy to a grayish-black or brown. The larvae feed at night and their presence in the soil is indicated by plants cut off at or below the surface of the ground. The moths are usually gray to brown. They fly at night and congregate at lights, where they may be readily trapped to determine their abundance in a locality. Among the most important species on corn in the United States are the black cutworm, *Agrotis ypsilon* (Rott.), the glassy cutworm, *Crymodes devastator* (Brace), the dingy cutworm, *Feltis subgothica* (Haw.) and the clay-backed cutworm, *Ag-*

rotis gladiaria (Morr.). These species are widely distributed in the United States and Canada, but vary in abundance in different areas. The black cutworm is world-wide in distribution and is of general importance on other crops (Forbes, 1905; Walkden, 1950; Stanley, 1936).

b. Habits and Biology. The incidence of cutworm larvae in cornfields is usually dependent on the populations present in the previous crop and the practices followed for seed-bed preparation. The moths

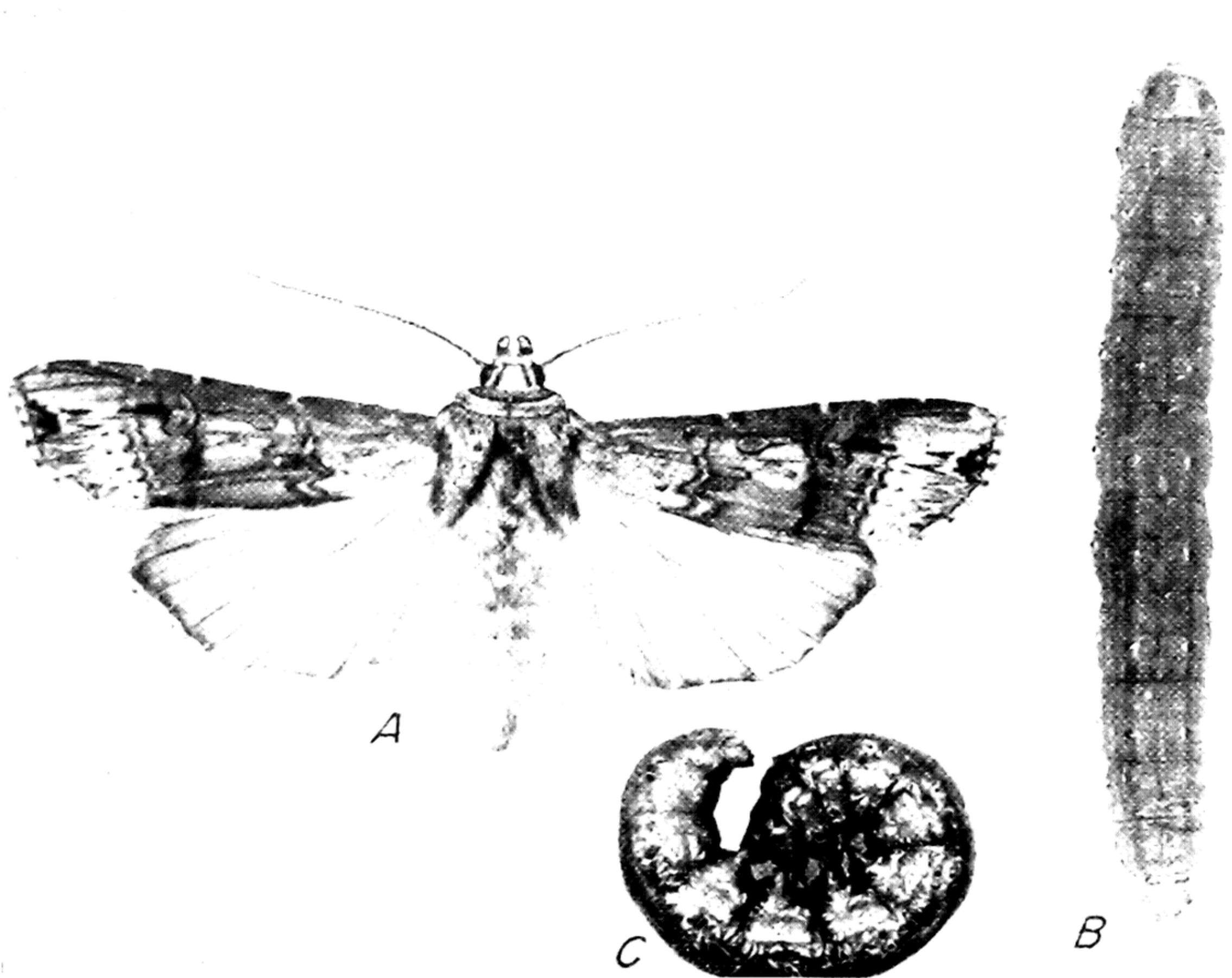


FIG. 5. The black cutworm. A, moth; B, larva extended; C, larva curled up.

deposit their eggs in hay or sod land early in the fall. The larvae generally develop on grass or clover and pass the winter about half-grown. They sometimes migrate to corn. The black cutworm, however, overwinters in the pupal stage in southern areas. It has two or more generations, depending on the bioclimate, whereas the other three species are single-brooded. Immature larvae are usually present in the field when the crop is planted. The larvae occupy burrows in the soil, feeding on plant parts that they have severed and pulled in from the surface. The girdling of plants is therefore a means to an end which results in a loss of plants out of proportion to the food requirements of the larvae. Loss of stand may be substantial even with a low population (Forbes, 1905; Crumb, 1929).

c. Cultural Practices. Late-summer or early-fall plowing to eliminate the young larvae has been recommended for many years. This

practice, however, is not desirable in hilly areas, where grass sod serves to prevent erosion of the soil through the winter. Under such conditions spring plowing is the logical practice. Most farmers replant when stands have been depleted by cutworm infestation.

d. Chemical Control Measures. A poisoned-bran bait evenly broadcast on the soil surface is effective on small areas (Walkden, 1950). In recent years good results have been obtained from toxaphene sprayed over the rows at the rate of 2 pounds per acre (Lilly and Gunderson, 1953).

4. Wireworms—Many Species

a. Description, Injury, and Distribution. Wireworms are the larvae of the common click beetles. They are slender, shiny, rather sluggish, buff to reddish-brown, heavily chitinized, and usually from $\frac{1}{2}$ to $1\frac{1}{2}$ inches long. Typical symptoms of their presence in corn are poor stands, dying seedlings, and tillering of young plants. In addition to corn the wireworms are injurious to small grains, forage grasses, and vegetable crops. The widely distributed species on corn are *Agriotes mancus* (Say), the wheat wireworm; *Melanotus cribulosus* (Lec.); *Aeolus mellillus* (Say); *Melanotus communis* (Gyll.); and *Horistonotus uhlerii* Horn, the sand wireworm (Forbes, 1893; Glen *et al.*, 1943; Thomas, 1940; Tenhet and Howe, 1939). The last species is of primary importance in sandy soils of southern states.

b. Habits and Biology. The wireworm problem in corn is inherited from the previous crop of pasture or forage grasses and in some cases, small grain. A generation is completed in one to three or more years, depending on the species. A typical generation develops as follows. The larvae pupate in earthen cells in middle summer. The adults emerge in the late summer and early fall. They remain in the pupal cells in the soil and emerge in the spring. The eggs are deposited in grass or small-grain fields and hatch in about two weeks. The young larvae feed on the roots until fall, when they burrow deeper into the soil for hibernation. They resume feeding on roots or sod during the following summer, go again into hibernation, and complete their feeding in the following spring. When corn is planted on infested ground, the immature larvae migrate to the germinating seed or young plants, burrow through the seed, and feed on the developing roots and crown (Fig. 6). Loss of stand therefore is the initial effect, particularly if large populations are present.

Tenhet and Howe (1939) found a one-year cycle of the sand wireworm in South Carolina, and Jewett (1942) reported a full and a partial second generation of *Aeolus mellillus* (Say) in Kentucky, with the

most injury from the overwintered larvae in the spring. *Agriotes mancus* (Say), *Melanotus communis* (Gyll.) and *M. cribulosus* (Lec.) are long-cycle species that sometimes injure corn (Hawkins, 1936; Hyslop, 1915). There appears to be general agreement that the wireworms attacking wheat and corn are favored by a moist clay soil with liberal



FIG. 6. Wireworms and typical injury to corn seedlings. (Courtesy of the Iowa Agricultural Experiment Station.)

amounts of organic matter. However, *Horistonotus uhlerii* Horn, an important species in the South, thrives in light sandy soils low in organic matter. In the Pacific Northwest several species of wireworms attack corn and other crops (Lane, 1941).

c. Cultural Practices. Until recent years cultural practices were considered the only means of relief for wireworm infestations. These practices varied with the species involved. Hawkins (1936) reported

that a short rotation and the use of crimson clover or buckwheat as a green manure crop reduced reinfestation. Clean cultivation and summer plowing or fallowing, regular crop rotation, and soil drainage have also been recommended, the objective being to eliminate susceptible vegetation and to disturb the insect activities as much as possible.

d. Chemical Control Measures. Insecticides and repellent substances have been under test for many years. Recently effective and practical control has been obtained with some of the new insecticides. On corn Lilly and Gunderson (1953) list two methods and three toxicants for chemical control—namely, lindane seed treatment for the lower levels of infestation and a soil application of either aldrin or chlordane followed by disking for high levels of infestation.

5. Billbugs (*Calendra* spp.)

a. Description, Injury, and Distribution. The billbugs are snout beetles. Most of them are reddish or brown, but they may appear grayish when covered with mud. They vary from about $\frac{1}{4}$ to 1 inch in length. The larvae are white with brownish heads, rather plump, and legless. Injury on young corn plants shows up as a series of transverse oblong or round holes in the leaves and some destruction of the growing point which results in excessive tillering.

As pests of corn billbugs are widely distributed and are often responsible for loss of stand and stunting of the plants. The species most injurious to corn in the United States are the maize billbug (*Calendra maidis* (Chitt.)), timothy billbug (*C. zae* (Walsh)), bluegrass billbug (*C. parvula* (Gyll.)), southern corn billbug (*C. callosa* (Oliver)), and destructive billbug (*C. destructor* (Chitt.)) (Forbes, 1905; Kelly, 1911; Satterthwait, 1932).

b. Habits and Biology. Most of the billbugs normally inhabit moist or swampy soil areas, where the larvae develop on various species of grasses such as rushes, sedges, reeds, timothy, and bluegrass. Infestations on corn, therefore, are likely to occur when this crop is planted in or near ground that had these conditions and plant associations in previous seasons. In some species only the adults are injurious, whereas in others, notably the maize and southern corn billbugs, the larvae also infest corn. Only a single generation occurs annually in the species commonly recorded on corn, the adults living over winter among the roots or in the roots or culms of their hosts.

In the spring the adults feed on bulbous parts or rhizomes of grasses. They begin to infest corn during the seedling and post-seedling stages of growth, eating small holes into the plants at about the soil surface, thereby piercing the rolled leaves in the bud. As the leaves unroll, they

show the typical transverse series of holes, which increase in size with the growth of the leaves. Severe injury in seedlings may cause distortion of the young leaves or even the death of the plants. In a study of the habits of *Calendra callosa* (Oliver) on corn in North Carolina, Metcalf (1917) found eggs deposited in plants near or below the soil surface and also among the roots. The eggs were laid in May or June. Larvae were found feeding in the plants and externally on the roots. This feeding resulted in the death of young plants and stunting when older plants were attacked. The injury caused by the larvae in the lower part of the stem was more serious than that caused by the adults. Similar observations were reported by Cartwright (1929) from South Carolina for *Calendra maidis* (Chitt.).

c. Cultural Practices. There appears to be general agreement that drainage of swampy areas and the elimination of the common wild host grasses associated with them will lessen the incidence of infestations on corn grown in or near such an environment. Rotation of crops, early planting, clean cultivation, and use of fertilizer are the normal practices that reduce injury and stimulate plant growth to overcome it (Metcalf, 1917; Satterthwait, 1932; Cartwright, 1929).

d. Chemical Control Measures. Lilly and Gunderson (1953) recommended spraying toxaphene over the corn row at the rate of 2 pounds per acre, as is done to control cutworms and sod webworms.

6. Sod Webworms (*Crambus* spp.)

a. Description, Injury, and Distribution. The adults of webworms are crambid or close-wing moths. The larvae are slender, yellow to pink with regular dark spots, and about 1 inch in length when full grown. When injury on young plants is first noticed, the larvae, then about $\frac{1}{2}$ inch long, are located in silken web-lined burrows in the soil near the plants. Typical attack at or below the ground level shows gnawed places, pits, or sometimes cut-off plants, somewhat resembling cutworm injury. Above the soil surface the infested plants have distorted leaves with ragged eaten places in them. Sod webworms are occasionally injurious to corn in the Corn Belt following spring plowing of sodland. The most common species injurious to corn are the corn root webworm (*Crambus caliginosellus* Clem.), striped webworm (*C. mutabilis* Clem.) and larger sod webworm (*C. trisectus* (Wlk.)) (Forbes, 1905; Ainslie, 1922).

b. Habits and Biology. According to Ainslie (1922), the corn root webworm has a single generation annually, whereas the striped webworm and larger sod webworm have at least two full generations. However, all three species pass the winter as partly grown larvae. The web-

worm moths drop their eggs in flight on bluegrass, timothy, and other grass sod. Thus, the development of larvae is closely tied up with grass sod and perhaps the legumes commonly found with it. Corn is a host only where it follows sod. The eggs from which the overwintering larvae develop are deposited in the summer. The young larvae establish themselves within their flimsy cocoons or webs in the sod, feed on foliage during late summer and early fall, and establish themselves in burrows in the soil before winter. They are about $\frac{1}{2}$ inch long. With warm weather in the spring, feeding is resumed, the larvae completing their development in about one month. When corn is planted on spring-plowed sod land infested with webworms, the seedling stage is attacked, resulting in loss of stand (Ainslie, 1922, 1927).

c. Cultural Practices. Cultural practices for controlling sod webworms have not been evaluated for many years. Late-summer or early-fall plowing has been recommended for eliminating the partially grown larvae before they enter hibernation. However, fall plowing would not be an acceptable practice on soils that are subject to erosion. Since most of the larvae become full grown while the corn is in the seedling stage, serious crop injury does not usually occur in corn that is replanted (Ainslie, 1922).

d. Chemical Control Measures. Chemical control of webworms has long been practiced on special sods such as lawns and golf greens. Noble (1932) described methods for controlling them with pyrethrum extracts and kerosene emulsion. Lilly and Gunderson (1953) recommend, as for cutworms, 2 pounds of toxaphene per acre sprayed over the rows of corn.

7. White Grubs (*Phyllophaga* spp.)

a. Description, Injury, and Distribution. White grubs are the larvae of brown beetles commonly known as May or June beetles. The larvae are sluggish, white, with brown heads and rather prominent legs (see Fig. 7). They have two slightly curved, narrowly spaced rows of spines on the ventral side of the last abdominal segment. Larvae feed on the roots of corn, causing stunted, wilting, or dying plants beginning with the seedling stage of growth.

There are many species of white grubs, which vary in abundance in different sections of the country. Chamberlin and Callenbach (1943) found the following species to be most numerous on cereal and forage crops in Wisconsin: *Phyllophaga rugosa* (Melsh.), *P. hirticula* (Knoch), *P. fusca* (Froel.), and *P. tristis* (F.) According to Luginbill and Painter (1953), these species are widely distributed and cause important crop damage.

b. Habits and Biology. The primary source of white grubs in corn-fields is soil that has been in grass and in some instances in soybeans. These plants serve as food for the grubs. Bluegrass and timothy sods are particularly favorable for their development. The beetles ordinarily prefer to feed on the foliage of trees, but they also feed on weeds and crop plants.

Most of the important species of May beetles require three years to complete a generation. Of the four species listed only *P. tristis* has a

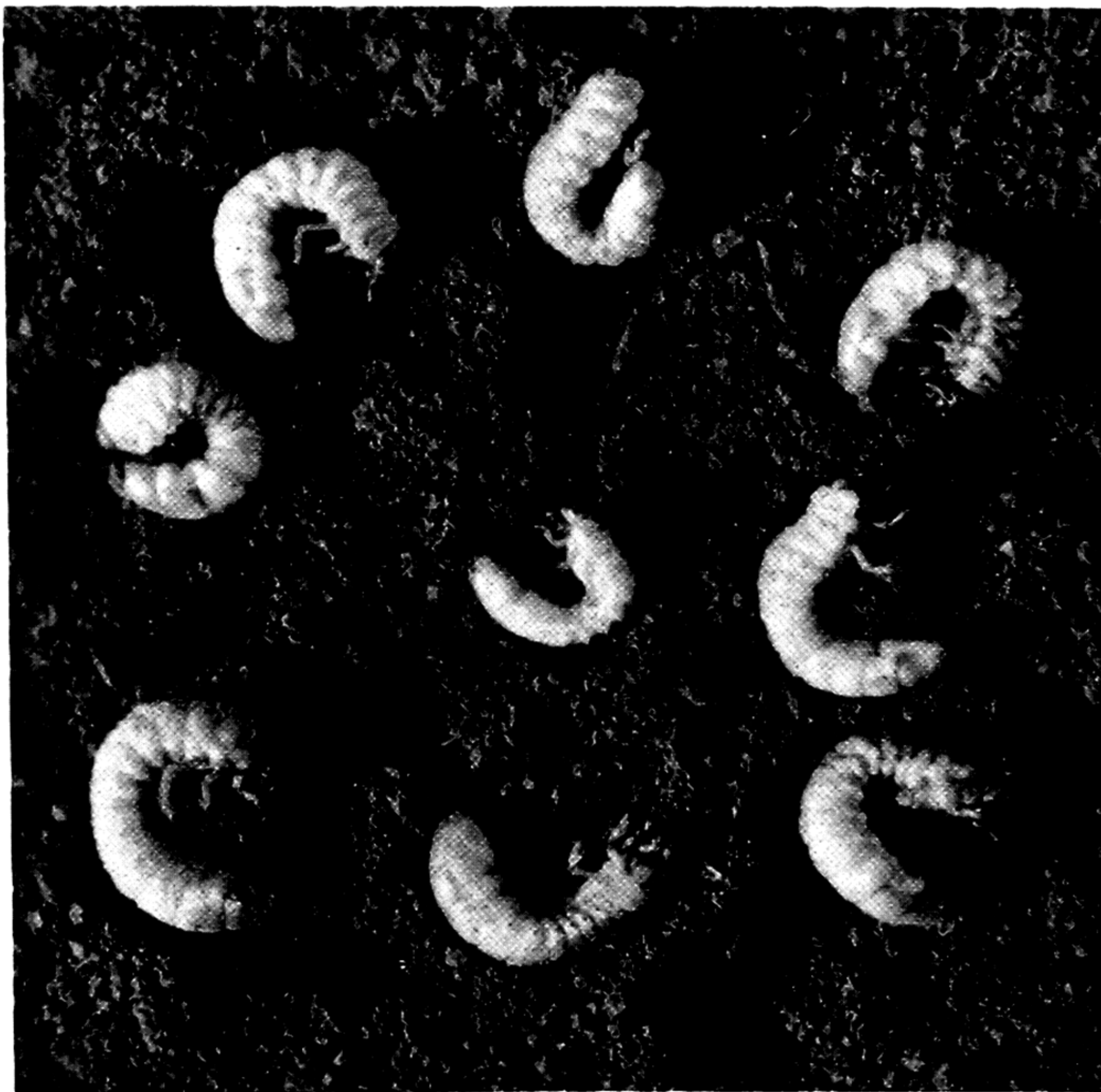


FIG. 7. Full-grown (3rd year) white grubs.

two-year cycle. The adults emerge from the soil in the spring and lay their eggs a few inches below the surface. The eggs hatch in about three weeks, and the young larvae feed through the first season on living roots and decaying vegetable matter at about plow-sole level or in the top soil. Late in the fall they burrow deeper into the soil and remain inactive during the winter. The second-year larvae feed throughout the growing season on the roots of plants; this is the stage most injurious to corn planted on infested sod ground. In the fall the larvae again go deep into the soil to overwinter. The feeding period in the third year is relatively short, pupation taking place in cells in midsummer and emer-

gence of the adults in the early fall. There is an overlapping of broods which results in beetle flights each year. For three-year-cycle species these broods are designated as A, B, and C. Brood A is by far the most abundant and is the one present in outbreak years. Brood B is usually unimportant, but brood C is sometimes injurious in certain areas.

When corn is planted in infested ground, the grubs congregate near the base of the plants, where they feed on and sever the young roots. Likely places of infestation are on high ground near wooded areas where the adults concentrate for their feeding. It is therefore not uncommon to find the important infestations associated with the poorer soils in an area (Davis, 1922; Luginbill and Chamberlin, 1953).

c. Cultural Practices. In areas where white grubs are periodically a problem, Luginbill and Chamberlin (1953) have proposed certain cropping practices utilizing crops that are least susceptible to attack. They suggest avoiding the common grasses as much as possible and using alfalfa and the clovers as the dominant pasture and hay crops.

An effective method of eliminating grubs from infested fields to be planted to corn is through pasturing by hogs. This practice is not desirable on permanent pastures because of the serious uprooting of the sod. Crows, blackbirds, skunks, and opossums also help to keep down populations of white grubs.

d. Chemical Control Measures. Several insecticides are effective against white grubs on field crops. Luginbill and Chamberlin (1953) recommend chlordane at the rate of 10 pounds per acre. Lilly and Gunderson (1953) recommend chlordane at the same rate and also aldrin or dieldrin disked in at the rate of 3 pounds per acre.

8. Corn Root Aphid (*Anuraphis maidi-radialis* (Forbes))

a. Description, Injury, and Distribution. The corn root aphid is bluish-green and about the size of a pinhead. It sucks the sap from the roots of corn and cornfield weeds. Typical external evidences of injury are dwarfing and yellowing and reddening of plants before they are knee-high, and ant burrows around the plants.

This aphid is widely distributed in the United States but is most abundant in the Corn Belt (Davis, 1949; Forbes, 1915).

b. Habits and Biology. The corn root aphid is dependent on ants, principally the cornfield ant. This aphid has both sexual egg-laying and parthenogenetic viviparous forms. The sexual form deposits the eggs in the fall, whereupon the ants transfer the eggs to their nests and nurture them during the winter. When the eggs hatch in the spring, the ants transfer the young to the roots of cornfield weeds and later, after corn is planted, to the roots of corn. The ants feed on the sweetish fluids excreted by the aphids. During the spring and summer the aphids re-

produce viviparously, some of the offspring being winged forms. The winged aphids emerge from the soil and fly to other fields, where with the attending ants new colonies are produced (Davis, 1949). Successive crops of corn, satisfactory spring host plants, and a favorable environment for the cornfield ant are important factors in building up populations.

c. Cultural Practices. The corn root aphid is of economic importance only on corn (Davis, 1949). Therefore, rotation of crops will hold down both aphid and ant populations. In the presence of both insects Bigger and Bauer (1939) found that plowing shortly before planting reduced aphid infestations, but that early plowing and tillage to keep favored wild hosts under control before planting corn was the most desirable practice. In connection with the other cultural practices Davis advocated thorough cultivation and maintenance of a high fertility level to stimulate plant growth.

d. Chemical Control Measures. Chlordane applied to the soil at the rate of 1 pound per acre is recommended for the control of both the corn root aphid and cornfield ants (Lilly and Gunderson, 1953).

9. Seed-Corn Maggot (*Hylemya cilicrura* (Rond.))

a. Description, Injury, and Distribution. The adult of the seed-corn maggot is a grayish fly similar to the house fly but with a more prominent thorax. The larva is pearly-white, almost conical, tapering anteriorly, and has black hooklike mandibles. When full grown it is about $\frac{1}{4}$ inch long. The larvae mine into the germinating seed in the ground, and later they also attack the young seedling.

The species is world-wide in distribution. In addition to corn it is an important pest of many vegetable crops (Forbes, 1893; Hawley, 1922).

b. Habits and Biology. The habits and biology of the seed-corn maggot have been studied mostly on vegetable crops. The adults are attracted to decaying vegetable or animal matter on which the eggs are deposited. The maggots attack the sprouting seed and seedlings. In the warmer parts of the country adults are abroad throughout the year. Reid (1940) reported that diapause was not observed in North and South Carolina, where he trapped adults every month of the year. He found puparia in the fields and also observed oviposition in the winter months. Hawley (1922) in New York reported collecting adults on wheat stubble in the spring and assumed that the insect spends the winter in the puparium. It is generally agreed that the maggots become injurious on seeds and seedlings under cool, moist soil conditions in the spring and fall.

c. Cultural Practices. As a pest of corn the infestations are most prevalent in early plantings on soils with liberal amounts of plowed-

under decaying plant material. Under such conditions, Hawley (1922) suggested that shallow planting and seed of good vitality to obtain germination as quickly as possible is the best means of avoiding stand failure.

d. Chemical Control Measures. Recent experimental work has shown that the same materials that give good protection against root-worms also are effective against the seed-corn maggot. Floyd and Smith (1949) reported substantial increases in stand and yield by applying BHC or chlordane mixed with 4-12-4 commercial fertilizer. In this mixture the BHC was applied at the rate of 1 pound of the gamma isomer, and chlordane at 5 pounds per acre. Three hundred pounds of the fertilizer containing these dosages of insecticides were applied per acre. Lilly and Gunderson (1953) recommend lindane seed treatment as a satisfactory maggot-control practice.

10. Sugar-Cane Beetle (*Euetheola rugiceps* (Lec.))

a. Description, Injury, and Distribution. The adult of the sugar-cane beetle, sometimes called the rough-headed cornstalk beetle, is black, about $\frac{1}{2}$ inch long, and similar in appearance to the common dung beetles. The main injury on corn is in the seedling and post-seedling stages of growth. The beetles feed on sprouting seed and gouge and gnaw through the leaf sheaths into the stem near the crown. Evidences of beetle injury are wilting or drying of the inner leaves of the bud and tillering of the plants that survive injury.

This beetle is an important pest in the southern states, where severe outbreaks sometimes occur. It is a pest of rice and sugar cane as well as of corn (Phillips and Fox, 1924; Baerg, 1942; Ingram *et al.*, 1951).

b. Habits and Biology. The larvae develop in soils with liberal amounts of decaying vegetable matter consisting mainly of various grasses, commonly *Paspalum* spp., Bermuda grass, and Johnson grass. Phillips and Fox (1924) observed infestations in such plant associations under moist or poorly drained soil conditions.

The beetles deposit their eggs in the soil from spring to early summer, depending on temperatures. The incubation period requires about two weeks, larval development from six to eight weeks, and the pupal period about two weeks. The beetles emerge in late summer and early fall, feed on the wild grasses, and overwinter in the soil.

With a substratum attractive to the beetles for oviposition there is little movement from infested fields. The damage done to corn planted in such fields is therefore associated with the oviposition habits of the beetle.

c. Cultural Practices. Phillips and Fox (1924) reported that frequent systematic rotation, keeping land well cultivated, and good drainage created an unfavorable environment for this beetle. They also advocated early planting and fertilization to stimulate plant growth, but Baerg (1942) did not concur in the advantage of early planting. Ingram *et al.* (1951), in connection with this pest on sugar cane, recommended elimination of the sod breeding areas and substitution of adapted legumes on them. No insecticide has yet been found to give satisfactory control of the beetle (Anonymous, 1954a).

11. *Grape Colaspis* (*Colaspis flavida* (Say))

a. Description, Injury, and Distribution. The grubs of the grape colaspis are white with brownish heads and thoracic shield; and about $\frac{1}{8}$ inch in length when full grown. Compared with the common white grubs, they are not as slender, have less prominent legs, and lack the two rows of spines on the last abdominal segment.

The adults are small, pale-brown beetles, which have many hosts but commonly feed on clover, beans, grape, and strawberry foliage.

The symptoms of injured plants are stunting and wilting, but under heavy infestations plants may be killed. Root injury begins on young plants and is characterized by dead surface tissue on the roots. The species, known also as the clover rootworm, is widely distributed east of the Rocky Mountains. It has been reported as injurious to young corn mainly in the North Central States (Forbes, 1905; Bigger, 1928; Lindsay, 1943).

b. Habits and Biology. Grubs on young corn usually originate from infestations in ground planted to clover, soybean, or timothy. The beetles emerge in midsummer and deposit their eggs in the soil. Incubation requires one to two weeks. The young larvae commonly become established and feed on the roots of clovers during the latter part of the summer and early fall. The winter is passed as immature larvae. With the appearance of warm weather in the spring, the larvae feed on roots, completing their development late in the spring.

Bigger (1928) reported the larvae to be most abundant on red clover, sweetclover, soybeans, and timothy, in the order named. The most severe injury on corn occurred when red clover ground was plowed late in the spring. Lindsay (1943) in seasonal-history studies in Iowa also reported damage to corn following red clover.

c. Cultural Practices. Metcalf *et al.* (1951) state that a rotation that will avoid planting corn on spring-plowed clover or timothy sod will nearly always prevent injury by this insect.

12. *Seed-Corn Beetles* (*Agonoderus lecontei* Chand. and *Clivina impressifrons* Lec.)

a. Description, Injury, and Distribution. The injurious forms of the seed-corn beetles are the adults. The adult of *Agonoderus lecontei* is oblong, about $\frac{1}{4}$ inch long, and dark with two brown stripes on its wing covers. The adult of *Clivina impressifrons* is slender, about $\frac{1}{4}$ inch long, and shiny dark-red, with a constricted articulation between the first and second thoracic segments. In characteristic injury the germinating seed is attacked, and the kernels have holes penetrating into them or are hollowed out, with dead or stunted sprouts. Both species are widely distributed in the United States and Canada (Forbes, 1893; Phillips, 1909).

b. Habits and Biology. The two species hibernate as adults. They are attracted to lights in large numbers, especially on warm evenings in the spring. The presence of beetles throughout the season indicates that there are one or more overlapping generations annually. Little is known of the habits of the immature stages. It is believed that the larvae are predaceous on other soil insects and may also breed in sod. The adults of *Agonoderus lecontei* are sometimes pests in lawns and golf greens. Both species occur in wet grassy ground (Forbes, 1893; Phillips, 1909; Hamilton, 1935).

c. Cultural Practices. In soils inhabited by these beetles Phillips (1909) suggested delaying planting until there is assurance of quick germination.

d. Chemical Control Measures. Lilly and Gunderson (1953) recommend the same lindane seed treatments as for control of the seed-corn maggot and wireworms.

IV. Insects Attacking the Leaf, Stalk, and Ear

Most of the insects injurious on the leaf, stalk, and ear may at some time feed on any of the major parts of the corn plant. The parts attacked depend to a large extent on the stage of plant development and on the life history of the insect. Some species may develop partially on the foliage and partially on the tassel in one generation, but in a subsequent generation entirely on ear structures. The group includes some of the most important corn insects.

1. *The Corn Earworm* (*Heliothis armigera* (Hbn.))

a. Description, Injury, and Distribution. The newly hatched larvae are light-gray with conspicuous small dark hairs. The full-grown larvae

range in color from red and brown to green with a striped appearance. They may be located in the bud or on the emerging tassel but are most frequently found feeding in the tip of the ears. The moths vary in color from a light olive-green to buff. The eggs, laid singly on the leaves, emerging tassel, and silks, are off-white, dome-shaped, with ribs converging at the top. Three stages of development are shown in Fig. 8.



FIG. 8. Different stages of corn earworm. Lower left, eggs; center, full-grown larva on the tip of the ear; upper right, adult moth.

The insect is world-wide in distribution, and because it also damages cotton, tomatoes, legumes and other crops, entomologists rate it as one of our most injurious insects.

b. Habits and Biology. For many years the corn earworm has received a great deal of attention by entomologists. Quaintance and Brues (1905) assembled the early information on the biology, distribution, and control of the insect as a pest of cotton. Many of the studies re-

ported by them are useful in an understanding of the earworm problem on corn.

The corn earworm hibernates as a pupa in a burrow prepared in the soil by the larva. Moths emerge from the pupae from early spring to early summer, depending on the bioclimate (Barber, 1936; Phillips and Barber, 1929). Early in the season oviposition by the moths is on the corn leaves and emerging tassel, but as the silks appear a high proportion of the eggs are deposited on fresh silks. Depending on the stage of plant development the young larvae become established on the leaves, in the whorl, on the florets of the tassel, or on the silks.

As the larva hatching on the silks or migrating there from other parts of the plant feeds and grows, it gradually infests the tip of the ear. When the husks are loose, feeding extends along the side of the ear. This type of feeding is especially prevalent on field corn in the more northern areas when the corn is in the dough stage. If the ear has a long husk extension and silk channel, the larvae sometimes mature on the silk. When feeding is completed, the larva leaves the ear, usually from the tip end or through an exit hole made through the husk. In the summer pupation takes place within a few days and moths emerge in two or three weeks, or they may have a period of estivation. The hibernating pupae become established in late summer and early fall. In the South there may be as many as five or six generations each year. In northern areas the earworm may have one or two generations annually, or perhaps there may be some infestation originating from migrant moths from farther south (Garman and Jewett, 1914; Barber, 1936; Ditman and Cory, 1931; Blanchard, 1942).

The attraction by the moths to the fresh silk for ovipositing results in a more or less regular shift of oviposition from the less attractive old to the more attractive new silks. This tends to limit larval development to corn before it reaches the dough stage for much of the growing season. On late-maturing corn there is a more prolonged oviposition, and more of the larvae mature on dough-stage corn. Because the larvae are cannibalistic, usually only one larva completes its development in an ear. Under high levels of infestation there may be a succession of larvae infesting the ears, particularly in the late summer and early fall. Eggs laid after the first week in September in Virginia are considered to be of little significance in the development of overwintering pupae (Phillips and Barber, 1929; Phillips and Barber, 1933; Dicke, 1939).

As corn becomes unattractive the moths move to other hosts for oviposition; particularly to cotton, tomatoes, and legumes. The importance of cotton or tomatoes in building up populations is not well known. Isely (1935) found that the reproductive capacity was highest

when the insect was reared on corn and lowest on tomatoes. In records covering 25 years he observed that this insect was most serious where the acreages of corn and cotton were about equal.

Hibernation of the earworm has received a great deal of attention because it is believed to have a bearing on the general abundance of the insect. The conditions that determine whether or not larvae will develop into estivating or hibernating pupae, the extent of successful hibernation, and seasonal abundance have been investigated in different parts of the country. The maturity of the corn on which the larvae feed may determine whether or not the pupae will hibernate and may affect the rate of overwinter survival. Phillips and Barber (1929) found that larvae maturing on dough-stage corn late in the summer developed into pupae that most successfully survived the winter. In hibernation studies conducted in southeast Georgia under cage conditions, Barber (1941) reported that an average of 51 per cent of the individuals that entered the soil for pupation in late summer and early fall survived to the following summer.

Ditman (1938) studied the water and fat relations of prepupae and pupae that developed from larvae reared on milk- and dough-stage corn. He concluded that the reduced percentages of water, the increased percentage of fat, and the reduced saturation of fat are intensified by a diet of dough-stage corn, and that these factors are associated with the ability of the earworm to withstand the temperature hazards of hibernating conditions. Some pupae from larvae reared on dough-stage corn were able to survive and produce moths after an exposure to temperatures of 15° to 18°F. for 10 days. In further studies Ditman *et al.* (1940) reported that diapause in the pupae may result when the larvae are exposed to low temperatures.

Experimental evidence shows that dry soil conditions favor survival of estivating as well as hibernating pupae (Barber, 1941; Barber and Dicke, 1939). From a study conducted near the District of Columbia it was concluded that a mean temperature of 30° F. or less from December through February reduced the abundance of the earworm the following season (Dicke, 1939). Blanchard (1942) summarized the results of co-operative hibernation experiments conducted in 15 central and northeastern states during the period 1935 to 1939. Survival of hibernating pupae was recorded in all of the states except Iowa. In Ohio and Indiana larvae entering the soil in October and early November showed a low rate of pupation. Eichmann (1940) reported a similar experience in Washington. The information at hand indicates that under conditions favorable for development and with a mild winter the earworm may hibernate farther north than has been supposed.

c. *Natural Enemies*. There is considerable mortality of hibernating pupae throughout the period from fall to summer. In soils where earthworms are abundant mortalities may be high when the pupae become embedded in the droppings deposited in the burrows. Diseases, particularly fungus, take a small toll. There is a rather low rate of parasitism and predation on larvae infesting the ear. *Trichogramma minutum* Riley frequently parasitizes a high proportion of the eggs, the amount of parasitism reaching a peak in the fall. Among the predators *Orius insidiosus* (Say) is responsible for exhausting a considerable proportion of the eggs deposited on silks (Phillips and Barber, 1929, 1933).

d. *Varietal Resistance*. The development of hybrids resistant to the corn earworm is receiving increased emphasis in the areas where the problem is of annual importance. In addition to resistance associated with husk protection, resistance to larval establishment and survival on the silks offers some promise (Walter, 1951). The last two factors would be desirable in all areas if they could be stabilized and transmitted to hybrids. The requirements for maturing the crop in the fall and for mechanical picking preclude the introduction of heavy husk cover in the more northern areas. From the standpoint of the corn breeder the problem is therefore more or less regional, the level of infestation being the limiting factor. Figure 9 shows a comparison of typical earworm injury under conditions of poor and good husk protection.

Through a long period of ear selection under a high level of corn earworm infestation southern open-pollinated varieties possess earworm resistance characters that are poorly developed on the ears of the more northern varieties, which have been exposed to a heavy earworm infestation only in an occasional year. Evidence of this is apparent in the results of some varietal tests made by Garman and Jewett (1914). Hinds (1914) pointed out that the extension and tightness of husk were qualities that provided protection against earworm injury and subsequent field infestation by the rice weevil. Collins and Kempton (1917) demonstrated that characters for resistance to ear infestation in field corn could be transferred to sweet corn and that husk extension and the number of husk layers were associated with protection against earworm injury. Kyle (1918) reported on the results of selections with such characters in connection with the development of varieties in Georgia. In a comparison of varieties of corn with different types of husk cover and extension, Phillips and Barber (1931) observed that ears protected by a long tight husk had less earworm damage and suffered less from grain beetles, grain moths, and birds. The varieties of southern origin gave the best protection against earworm injury.

In breeding and testing programs conducted co-operatively by State

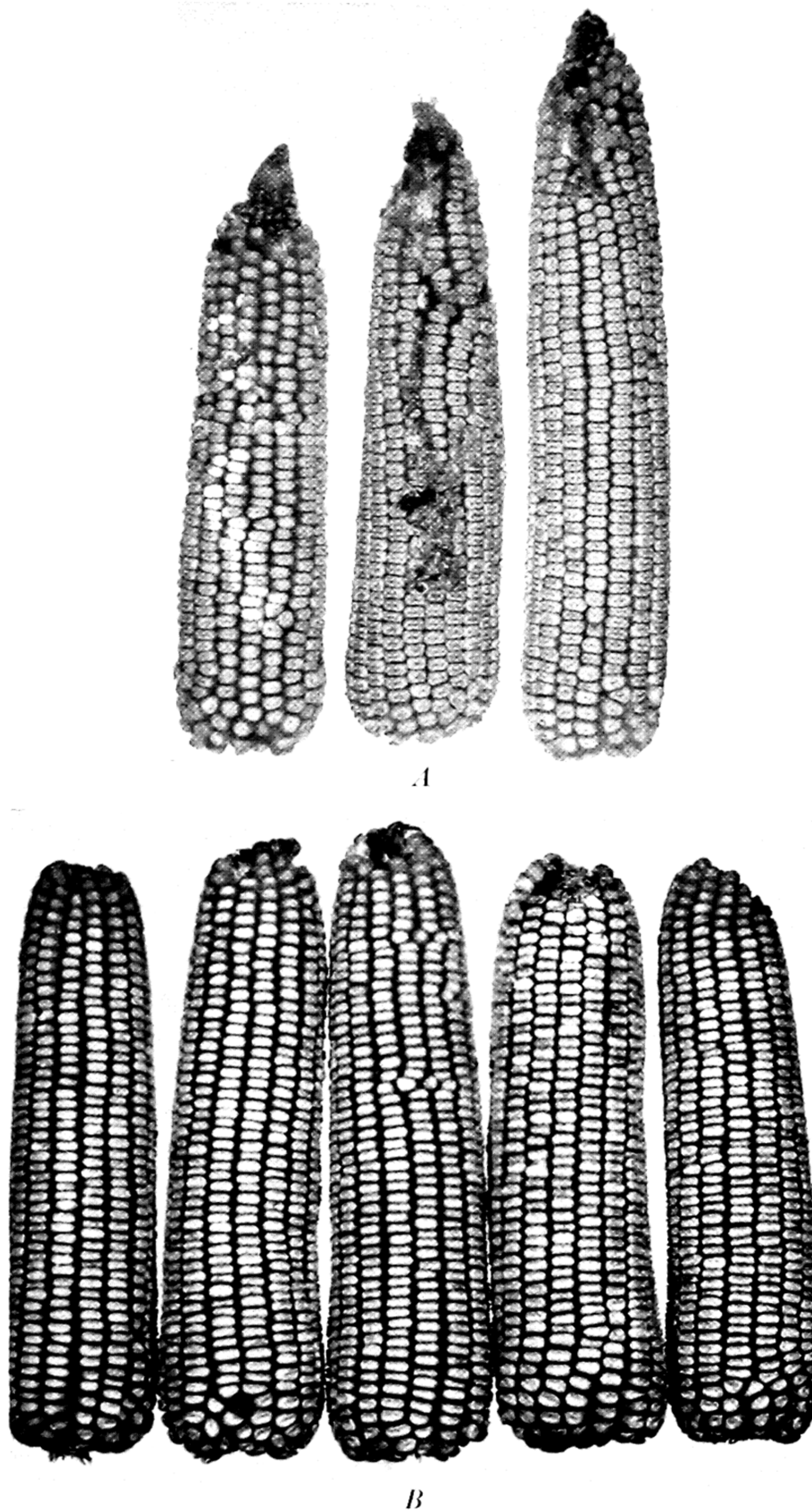


FIG. 9. Ears of a hybrid showing typical earworm injury under conditions of *A*, poor husk protection and *B*, good husk protection.

and Federal agencies a large number of lines have been evaluated for earworm resistance in recent years. The most reliable method for making these evaluations has been in hybrid combinations, particularly single crosses. Commercial hybrids adapted to the South which contain earworm-resistant lines in their pedigree are DIXIE 18, DIXIE 11, GEORGIA

281, and LOUISIANA 521. In Texas the yellow hybrids TEXAS 24 and 30 and the white hybrids TEXAS 9w and 11w are reported to possess some earworm resistance (Painter and Brunson, 1940; Blanchard *et al.*, 1941; Dicke and Jenkins, 1945; Douglas, 1948; Blanchard and Douglas, 1953).

e. Cultural Practices. One of the earliest recommendations for control of the corn earworm was fall plowing. It was recommended many years before definite evidence of its effectiveness for destroying hibernating pupae was available. Experiments in Virginia (Barber and Dicke, 1937) showed that fall plowing resulted in a high mortality of overwintering pupae. Spring plowing and fall disking were less effective.

The effect of planting date on the amount of earworm injury has been studied at several points. In Virginia tests early-planted corn produced the best yield and had a low rate of earworm damage. Similar observations in Georgia have confirmed these results (Phillips and Barber, 1934; Barber, 1936).

f. Chemical Control Measures. Combinations of mineral oils and insecticides are being recommended for control of the corn earworm in sweet corn, and such treatments are practical in seed corn production under heavy infestations. The best control is being obtained with DDT or TDE. Sprays are more effective than dusts. The number and timing of applications and the type of equipment require adjustment with the type of crop and intensity of infestation on a regional or local basis (Barber, 1942, 1944; Blanchard and Chamberlein, 1948; Kelsheimer *et al.*, 1950; Wene *et al.*, 1952; Hayslip *et al.*, 1953; Bacon *et al.*, 1953; Douglas and Smith, 1953; Blanchard and Wene, 1953; Blanchard and Douglas, 1953).

2. European Corn Borer (*Pyrausta nubilalis* (Hbn.))

a. Description, Injury, and Distribution. The newly hatched larvae of the European corn borer are about $\frac{1}{16}$ inch in length. The larvae are light-green after early feeding, with brown-to-black heads, but later take on a more opaque greenish-gray or pink color and have light longitudinal lines along the body. The full-grown larva, shown in Fig. 10, is about 1 inch long and varies in color, usually grayish to light-brownish, and frequently with a reddish tinge.

The pupae are $\frac{1}{2}$ to $\frac{3}{4}$ inch long, slender and brown. They may be located on the foliage, in the ears, or in the stalk in midsummer, and in surface debris in the spring. The moths are buff to brownish, frequently with reddish wing veins and a wing expanse of about 1 inch.

Descriptions of all the stages have been published by Vinal and Cafrey (1919).

Injury indicating the presence of larvae are shot-hole and elongated lesions on the leaf blades, burrows in the midribs and sheath, broken

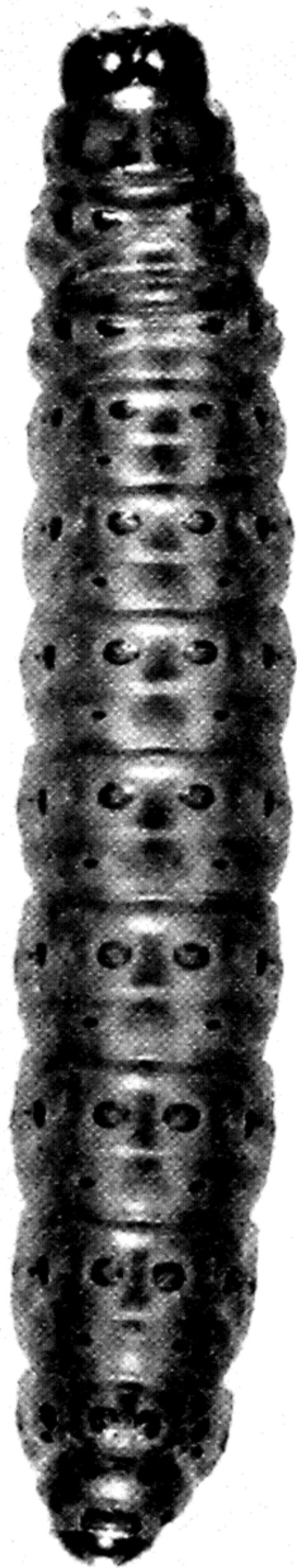


FIG. 10. Mature larva of the European corn borer.

tassels, and holes and burrows in the stalk. Figure 11 shows typical early first-brood infestation in the whorl stage of growth.

The presence of the European corn borer in the United States was first reported by Vinal (1917) in Massachusetts. Shortly afterward infestations were found in New York and Pennsylvania, 1919, Ontario, Canada, 1920, and Ohio, 1921. Separate points of introduction from foreign sources or spread through transportation were indicated in this

rapid westward establishment. Severe damage occurred in Kent and Essex counties, Ontario, in 1925 and 1926 and caused an appreciable reduction of corn acreage (Caffrey and Worthley, 1927; Stirrett, 1938). Movement westward and southward was gradual between 1927 and 1936. After the drought year of 1936 the spread into southern states and



FIG. 11. Typical leaf injury by first-brood larvae of European corn borer in a susceptible dent corn hybrid.

across the north central region proceeded more rapidly, and the insect reached the Rocky Mountains in 1950. The general abundance of the borer touched a peak in 1949, when there were high populations over much of the Corn Belt. The status of distribution and abundance for 1953 was reported by Shotwell (1954).

b. Habits and Biology. There are numerous published accounts on the biology and habits of the European corn borer. The results of ex-

periments and observations reported from certain areas may seem at variance with those of other areas. These differences are primarily due to differences in the environment and the population complexes produced in it. It is possible only to give a general discussion of the biology of the insect under the more usual circumstances that prevail over the infested areas.

The first extensive report on life-history studies in the United States was made by Vinal and Caffrey (1919). Most of this work was done on sweet corn and with an insect that was predominantly two-brooded. Their descriptions of the biology are in general still applicable to a two-brooded infestation similar to what they encountered in Massachusetts. Under a single generation, which was predominant for many years in the Great Lakes area, similar data were brought together by Crawford and Spencer (1922), Caffrey and Worthley (1927), and Huber *et al.* (1928).

The European corn borer hibernates as a full-grown larva in cornstalks or plant debris. Time of pupation and moth emergence in the spring depend on the weather and to some extent on whether or not the prevailing population is single- or multiple-brooded. For most of the infested area moth emergence begins in May or June. Most of the eggs are deposited between dusk and midnight. The important factors limiting moth activity are low temperatures and high winds. The earliest planted corn is most attractive to the moths of the first brood for oviposition, whereas late-planted corn is more attractive to the moths of the second brood. The stage of development of corn is therefore an important factor in the rate of oviposition and figures prominently in determining the need for the application of insecticides (Barber, 1925; Huber *et al.*, 1928; Stirrett, 1938). In a given area the stage of development of the corn crop varies widely during the first-brood egg-laying period. The vegetative or whorl stage of growth increases progressively in attractiveness and susceptibility to larval establishment and survival as plant growth increases.

The most significant increase in susceptibility occurs with the exposure of the tassel. A high susceptibility to larval survival persists throughout the reproductive stages of the plant but recedes significantly about two weeks after silking. This condition prevails in early-market sweet corn during the first-brood oviposition period in varying degrees and in late-maturing field and sweet corn during the second-brood oviposition period. The pattern of larval survival during the vegetative and reproductive stages of growth is shown in Fig. 12.

In the vegetative or whorl stage of growth the primary place of larval establishment is near the upper limits of the surface moisture

level on the spirally rolled leaves. The larvae are predominantly sheath and midrib feeders during the third and fourth stages, whereas the later stages invade the stalk, shank, and the ear.

During the reproductive stage of corn development, when they are present either during first- or second-brood oviposition, the young larvae become established largely on the structures associated with the inflorescence, in the florets, on pollen accumulations at the axils of the leaves, or on ear structures. The pattern of feeding by the middle- and late-stage larvae is about the same for both broods, with perhaps a

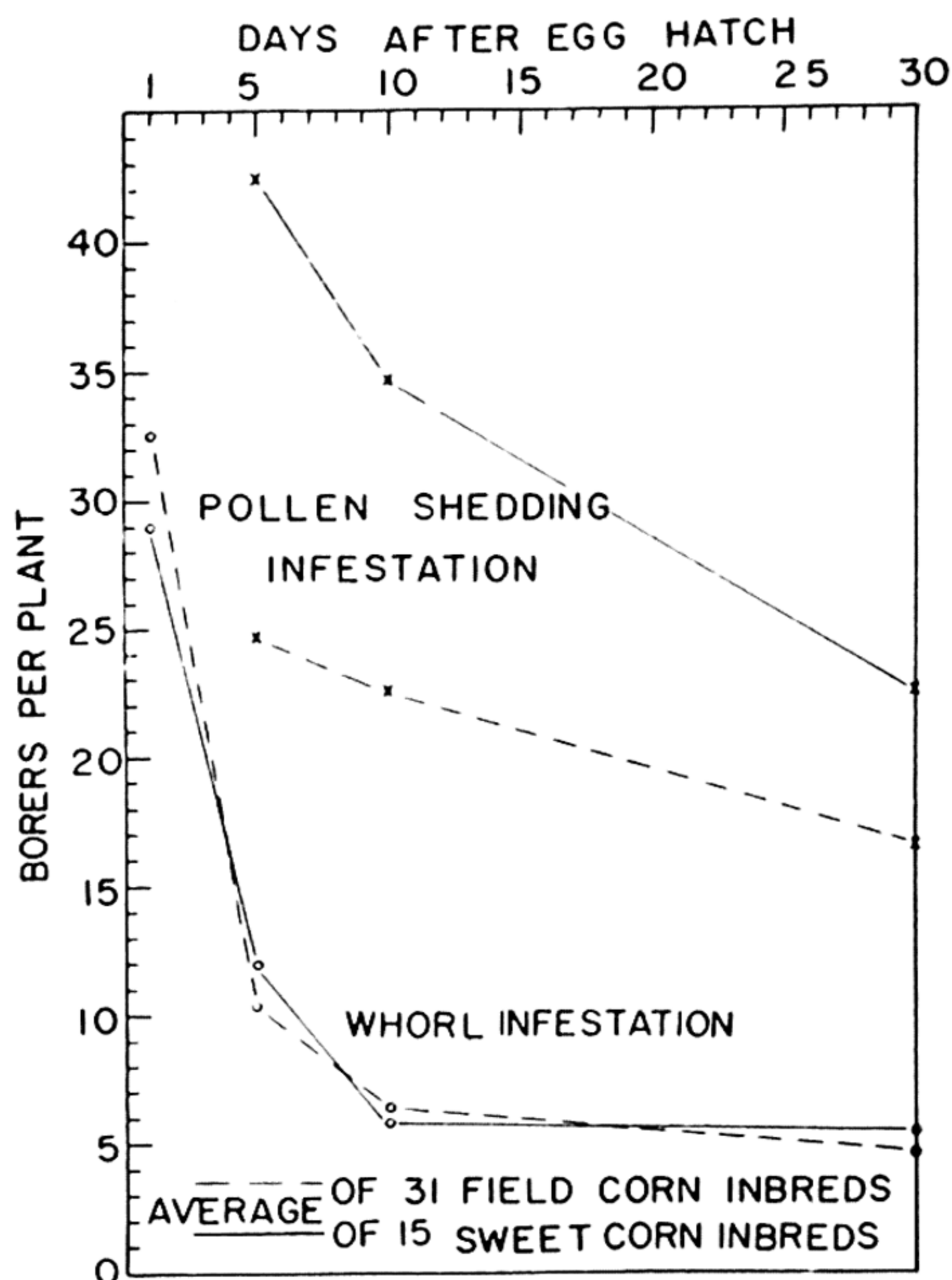


FIG. 12. Larval survival on field and sweet corn infested at different stages of growth.

higher concentration of young larvae in the upper region of the plant during the second-brood infestation. The full-grown larvae have a habit of establishing themselves in the lower part of the stalk (Caffrey and Worthley, 1927; Batchelder, 1949).

c. Biological Control. The United States Department of Agriculture established its program of foreign parasite introduction from Europe in 1919 and from the Orient in 1927. With the establishment of certain of the parasites in the older infested areas Federal and State agencies participated in redistribution and recovery programs of the most effective species. Baker *et al.* (1949) brought together the significant information on the biological control of the corn borer in the United States and

Canada. They reported the following introduced species as permanently established: *Lydella stabulans grisescens*, R. D., *Horogenes punctorius* (Roman), *Macrocentrus gifuensis* (Ashm.), *Sympeisis viridula* (Thoms.), *Chelonus annulipes* Wesm., and *Phaeogenes nigridentis* (Wesm.). Arbuthnot (1953), in reviewing the status of parasites in the United States, reported *L. stabulans grisescens*, *S. viridula*, *H. punctorius*, and *M. gifuensis* to be widely established, and *L. stabulans grisescens* to be abundant over most of the infested area.

The most common predators are several species of lady beetles, the hemipteron *Orius insidiosus*, and the downy and hairy woodpeckers.

d. Varietal Resistance. The first tests on varietal resistance showed that the early varieties of sweet and flint corn supported higher populations of larvae than the longer seasoned dent varieties (Crawford and Spencer, 1922; Caffrey and Worthley, 1927). Huber *et al.* (1928) found differences in the larval population and in the ability of some varieties to tolerate damage. In tests of F_3 and F_4 lines extracted from crosses of Maize Amargo and local Michigan varieties, Marston (1931) reported higher populations of larvae on the local varieties than on the recovered lines. Continued tests of selections of some of these lines have consistently shown a good level of resistance to survival of first-brood larvae.

With the advent of extensive breeding programs by Federal and State agencies in field, sweet, and popcorn there has been extensive testing of inbred lines and hybrid combinations of them. The results of these tests have been reported by Patch *et al.* (1942), Patch and Everly (1945), Schlösberg and Baker (1948), Meyers *et al.* (1937), and in special reports of Federal and State agencies.

It was established that resistance and tolerance qualities of certain lines were transmitted to their crosses and that there was a significant positive correlation between stalk breakage in the absence and presence of an infestation. Hybrids had less stalk breakage than open-pollinated varieties and lost less yield as a result of first-brood infestation (Patch, 1937; Patch *et al.*, 1941). In a comparison of the development of first-brood larvae on susceptible and resistant crosses, Patch (1943) reported slower development and smaller larvae on the resistant cross. Patch's data also show that with tassel appearance, pollen shedding, and silking both these single crosses become highly susceptible to larval survival—a condition that applies to early-market sweet corn during the first-brood infestation and in varying degrees to late-planted sweet corn and dent corn during the second-brood period.

Since the second brood tends to develop when most corn is rapidly approaching maturity, the direct loss in yield is not as serious as the

harvesting problem resulting from ear dropping and stalk breakage. The association of stalk rot with borer damage is discussed in a later section. In the breeding programs particular emphasis is being placed on combining resistance to larval survival and resistance to stalk breakage and ear dropping (Dicke and Penny, 1952).

e. Cultural Practices. The reduction of population levels through the disposal of infested crop residues was advocated in central Europe as early as 1897 (Babcock and Vance, 1929). Similar practices were later adopted in the United States and Canada (Vinal and Caffrey, 1919; Caffrey and Worthley, 1927). Much of the larval population of a given season is destroyed by the usual farm tillage and harvesting practices. The most effective reductions of the overwintering populations can be obtained through ensiling, shredding, or husking machines and by plowing under the crop residue so as to leave as clean a surface as possible (Baker and Bradley, 1948; Anonymous, 1952).

On the basis of a 10-year study of the effect of farm practices on the reduction of corn borer populations from October to June in Illinois, Bigger and Petty (1951) presented data to show that the general practice of disking stalk fields for oats is an important factor contributing to the continued threat of corn borer damage. Eighty per cent of the larval population in the spring after tillage were found in the disked fields. These authors advocated a tight adjustment of corn picker rolls and heavy pasturing of stalk fields as supplementary to good plowing, the most effective cultural control practice.

Early in the biological studies of the European corn borer it was established that under univoltine (single-brooded) infestation the earliest planted corn receives the highest rate of egg deposition and infestation and the latest planted corn the least. Under bivoltine infestation, where two broods prevail, the late plantings are likely to suffer from the second brood (Caffrey and Worthley, 1927; Huber *et al.*, 1928). In the areas that were subject to univoltine infestation delayed planting was encouraged. With the usual prevalence of a high bivoltine population in much of the corn-growing area, the planting dates that produce best results in a particular locality are advocated. In areas that are subject to summer drought or where a full season is required to mature a crop, the time of planting depends on seasonal conditions that are favorable for securing a satisfactory stand. Midseason planting of sweet corn can be timed so as to escape most of the first-brood infestation (Anonymous, 1952; Decker and Bigger, 1949).

f. Chemical Control Measures. In the early research programs insecticides in common use were tested extensively. The most effective ones were certain derris (rotenone), nicotine, and fluorine formula-

tions. In general sprays gave better results than dusts. The fluorine compounds caused varying degrees of chlorosis in corn. The importance of timing applications with respect to the seasonal development of the insect in relation to stages of plant growth was established (Batchelder and Questel, 1931; Simanton *et al.*, 1931; Batchelder *et al.*, 1937; Baker and Questel, 1939). Ryania dusts and sprays were introduced by Pepper and Carruth (1945). Recently many investigators have reported on tests of chlorinated hydrocarbon and organic phosphorus compounds. Of these DDT is presently the most commonly used toxicant. With the high susceptibility of early-market sweet corn and the high market



FIG. 13. Control of European corn borer by insecticides; left, heavily infested check rows; right, untreated rows.

value of premium grades, treatment with insecticides has become a necessity in areas where this crop is extensively grown. Similarly, canning corn, with its susceptibility to contamination of the pack, requires careful consideration for insecticidal treatment. Profitable insecticidal treatment of dent corn depends largely on the level of infestation and the value of the crop. The desirability for treatment, the material, timing, and equipment should be determined on a local basis (Anonymous, 1952). Figure 13 shows the effect of insecticide control on dent corn under a heavy infestation.

3. Fall Armyworm (*Laphygma frugiperda* (J. E. Smith))

a. *Description, Injury, and Distribution.* The young larvae of the fall armyworm are slightly greenish with black heads. They are com-

monly found feeding on the leaves in the buds of young corn plants. With the emergence of the tassel they feed on the tassel buds and surrounding leaves. Later the ear is favored (Fig. 14).



FIG. 14. Ear injury by the fall armyworm.

The mature larvae vary from greenish to grayish-brown and have a light-colored inverted Y on the head and dorsal lines running lengthwise of the body. The moth has variegated gray forewings, which are held at an angle over the back when at rest.

The fall armyworm is an important pest of corn and other grasses in the South Atlantic and Gulf states and periodically spreads to the

Middle Atlantic States and the southern part of the north central region, where it becomes prevalent in the later maturing corn in August and September. It has been observed as far north as Canada (Forbes, 1893; Luginbill, 1950).

b. Habits and Biology. The fall armyworm overwinters in subtropical and tropical America and migrates northward each year by moth flight as the season warms up. Diapause or estivation is not known to occur in any of its life stages. On corn the eggs are usually deposited on the under side of the leaves in large masses covered with the scales and hair of the moth. On hatching the young larvae feed on the tender parts of the whorl leaves, on the florets, young ear shoots, or fresh silk, the plant development being an important factor in the feeding habits of the larvae. The feeding habits are similar to those of the corn earworm and European corn borer. When the larvae become established in the whorl, the unfurled leaves show irregular elongated feeding areas. The older larvae may also feed behind the sheath and into the stalk.

With the appearance of the ear the larvae feed on the husks, in the shank, and on the silks, and also attack the kernels. The injury at the tip of the ear can easily be confused with that caused by the corn earworm. On becoming full grown the larvae leave the plant and prepare short tunnels and elliptical cells in the soil in which to pupate.

It requires about a month to complete a generation. In the South there may be as many as six generations annually, whereas in the more northern areas there may be only a single brood of larvae resulting from migrant moths (Luginbill, 1928, 1950; Dicke and Jenkins, 1945; Burkhardt, 1952).

The fall armyworm has several important hymenopterous and dipterous parasites as well as hemipterous and coleopterous predators. Some of the common entomogenous fungi have also been recorded in several localities in the South (Luginbill, 1928; Vickery, 1929).

c. Varietal Resistance. Little information is available on varietal resistance. Some inbred lines of dent corn are less subject to ear attack through the husks and through the silk channel than others. In areas where the fall armyworm is important the corn earworm is usually dominant. Therefore, it is necessary to consider the resistance of corn to both insects. In tests conducted in Virginia it was apparent that northern inbred lines in general are much more subject to fall armyworm attack on the husks, ear, and in the shank than some lines having southern corn in their parentage. Figure 15 shows differences in susceptibility to ear attack in two inbred lines of corn.

d. Chemical Control Measures. Blanchard (1951) found certain insecticides to be more effective against the fall armyworm than against

the corn earworm in ear infestations. Two applications of $1\frac{3}{4}$ to 2 pounds of DDT or 2 pounds of TDE in emulsion with $2\frac{1}{2}$ gallons of white mineral oil at 35 gallons of liquid per acre controlled both insects. Kelsheimer *et al.* (1950) summarized a seasonal program for the control of insects on market sweet corn in Florida, with different formulations of DDT and toxaphene. Brett (1953a) found endrin to be the most effective toxicant when applied at weekly intervals for six weeks at 2 ounces per acre. The application of insecticides against the fall armyworm depends on the location of the infestation (bud or ear) and the



FIG. 15. Difference in susceptibility of inbred lines of field corn to the fall armyworm: A, inbred line 38-11 with severe husk, ear, and shank injury; B, inbred line CI.7 with relatively little ear injury.

complex of insects present. Formulations, timing, and equipment require adjustment with the type of crop and more or less with conditions of the locality.

4. Southern Corn Borers (*Diatraea* spp.)

a. Description, Injury, and Distribution. The larval forms of the southern cornstalk borer (*Diatraea crambidoides* (Grote)) and the southwestern corn borer (*D. grandiosella* Dyar) and the injuries they cause are similar. The young larvae are dull-white to yellowish with black heads, about $\frac{1}{16}$ inch long, with prominent transverse closely spaced dark spots giving the general appearance of a ring around each

segment. With successive molts the dark spots are further apart, becoming pale shortly before pupation. In the winter form the larvae practically lose their spots and the black spiracles are very prominent.

The larvae of the sugar-cane borer (*Diatraea saccharalis* (F.)) are superficially very similar. Ordinarily they can be differentiated from



FIG. 16. First-brood injury by the southwestern corn borer. (Courtesy of the Kansas Agricultural Experiment Station.)

crambidoides by their brown spots. In the literature the two species were confused until about 1911. Typical injury by the larvae of the first broods of *crambidoides* and *grandiosella* is at first in the bud on the unrolled leaves (Fig. 16). As the leaves grow and unfold, the midribs are frequently invaded. Holes across the leaves and broken midribs are characteristic of later stages of leaf injury.

Severe injury to young plants may kill the bud, causing dead heart

and subsequent tillering. Holes are made in the stalks by the older larvae. The symptoms of second- or third-brood feeding on corn that has tasseled are sheath injury and holes and burrows in the stalk. Girdled stalks are more typical for the southwestern corn borer. Several insects over the general range of these stalk borers cause similar plant injury, the most common ones being the corn earworm and the fall armyworm.

The moths of the three species are of pale-to-medium straw color with white hindwings and a spread of about $1\frac{1}{4}$ inches. They are generally distinguished by the spots in the forewings. The southern cornstalk borer moths have a prominent black spot in the middle of the wing and seven similar spots along the margin. These spots are V-shaped in the moth of the sugar-cane borer and not conspicuous in the moth of the southwestern corn borer.

The southern cornstalk borer is generally distributed over the southeastern part of the United States and occurs as far west as Texas, Oklahoma, and Kansas. It has been ranked among the most important pests of the corn crop in the south Atlantic coastal region. The southwestern corn borer is distributed over the southwestern states east to Arkansas and Missouri and north to Colorado and Nebraska. Present eastward movement of its range indicates that it may become adapted to the Gulf states. The sugar-cane borer is of most importance on corn in the sugar cane and rice producing areas of the Gulf states (Ainslie, 1919; Leiby, 1920; Davis *et al.*, 1933; Cartwright, 1934; Ingram and Bynum, 1941; Wilbur *et al.*, 1950).

b. Habits and Biology. The habits and biology of the three species of *Diatraea* are sufficiently similar as far as the corn crop is concerned to permit a general discussion. The southern cornstalk borer and the southwestern corn borer hibernate as full-grown larvae in the stalk near the base or crown, sometimes erroneously called the tap root. Figure 17 shows the usual position of the hibernating larva of the southwestern corn borer. The larvae of the sugar-cane borer overwinter in various parts of the stalk but seldom below the level of the ground. The overwintered larvae pupate in the spring, the pupal stage requiring about three weeks. The time of first-brood pupation and moth emergence varies with the bioclimate from April to June. The eggs are normally deposited in masses under the leaves or on the sheaths in fish-scale fashion. The young larvae feed in the whorl of unfolding leaves, following a pattern similar to that of several of the other lepidopterous caterpillars occurring on young corn. They invade the growing point or they burrow in the stalk. There is a tendency for the larvae to leave the upper part of the stalk and to re-enter at lower points.

In the second and third broods the feeding habits of the young larvae depend on the development of the corn. On late-planted corn in the whorl stage of growth the habits are the same as those of the first brood, whereas on the older tasseled corn there is little feeding on the leaf blades but on the sheath and midrib, and again the older larvae feed and burrow in the stalk.

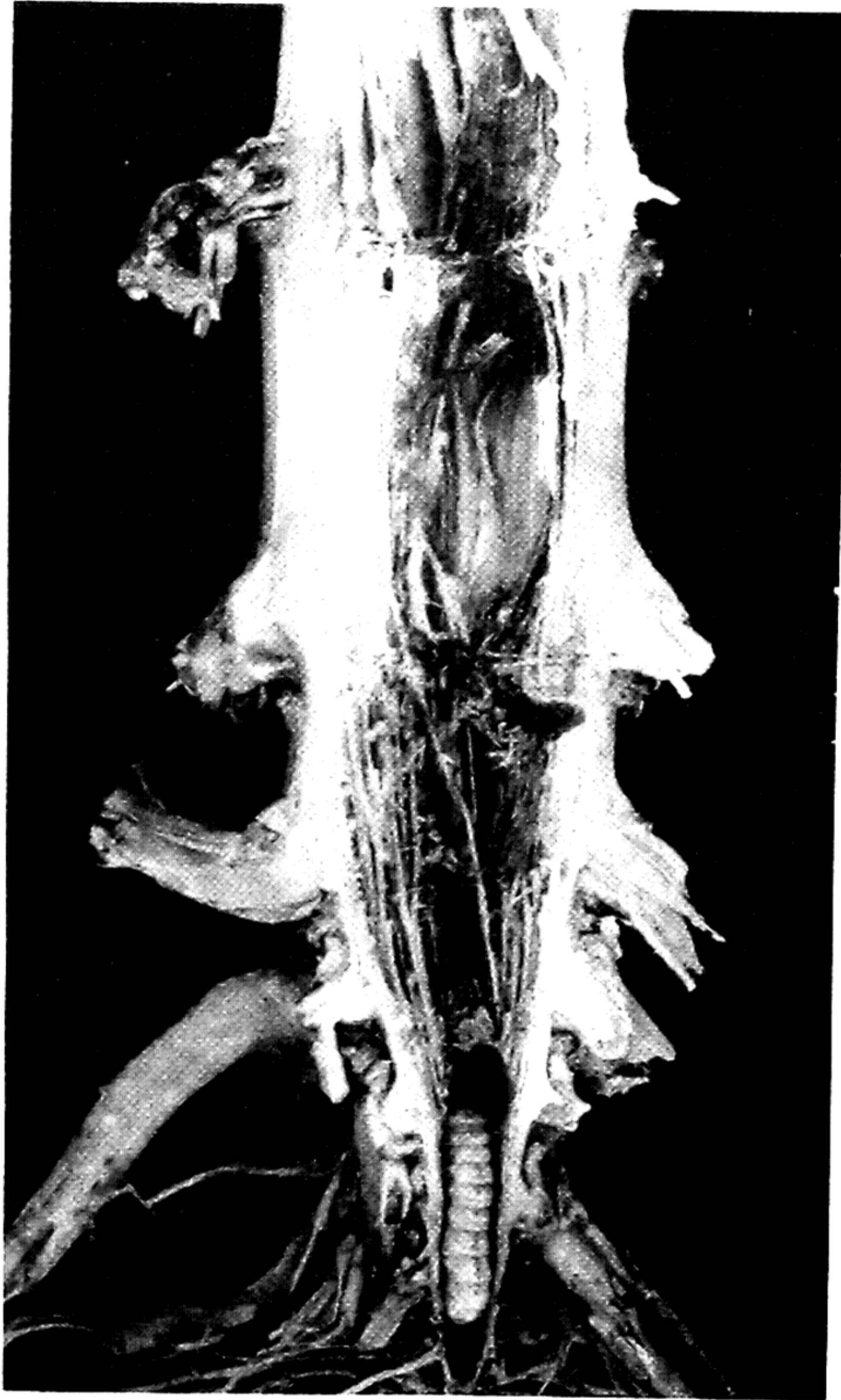


FIG. 17. Winter form of the southwestern corn borer in typical position for hibernation.

Phillips *et al.* (1921) reported two generations for *Diatraea crambidoides* in Virginia, and Cartwright (1934) recorded mostly two or three overlapping generations in South Carolina; this is similar to the observations on *grandiosella* by Walton and Bieberdorf (1948) and Wilbur *et al.* (1950). When three generations occurred, each of the first two produced some hibernating larvae. In the sugar-cane borer Ingram and Bynum (1941) report from two to four generations. Of particular significance in the second-brood infestations of the southwestern corn

borer is the severe breakage caused by larvae girdling the rind of the stalk usually below the ear. This has not been reported as serious in connection with the southern cornstalk borer.

c. Cultural Practices. Cultural practices advocated for reducing the populations of the southern cornstalk borer and the southwestern corn borer are very similar. They are aimed at eliminating as many of the overwintering larvae as possible by exposure of the infested corn stubble to freezing temperatures on the soil surface. A high percentage of the larvae are killed by subfreezing temperatures. The stubble or stalks should be plowed or disked out in the fall and allowed to remain on the surface until March. High mortalities among the hibernating larvae also result when stalks are scattered and broken up in such operations. Moths fail to reach the soil surface when the stalks are plowed under to a depth of 4 inches (Phillips *et al.*, 1921; Davis *et al.*, 1923; Cartwright, 1934; Wilbur *et al.*, 1950).

The southwestern corn borer has been most troublesome in the areas where grain sorghums are better adapted than corn. Wilbur *et al.* (1950) therefore advocated the substitution of sorghums for corn. This has already become a common practice in Oklahoma (Walton and Bieberdorf, 1948). In a study of planting dates a partial escape from infestation by the first brood was observed by these workers and also by Davis *et al.* (1933). In South Carolina Cartwright (1934) observed lower infestations of *Diatraea crambidoides* in late-planted corn, but discouraged this practice in areas where billbugs and the lesser cornstalk borer are important factors. He also observed that properly fertilized corn will outgrow injury and produce fair yields.

Ingram and Bynum (1941) regarded the source of the sugar-cane borer as a pest of corn to be sugar-cane debris and rice stubble. A high percentage of the overwintering larvae may be destroyed by burning the sugar-cane trash. In rice stubble the hibernating larvae are materially reduced by grazing, burning, flooding, and dragging.

d. Chemical Control Measures. In tests with methoxychlor, DDT, isodrin, and endrin, Brett (1953b) reported endrin as the most satisfactory material to control the southern cornstalk borer. Several spray applications of 0.12 pound per acre of either isodrin or endrin eliminated larvae in the stalks, but endrin showed the least phytotoxic effect.

5. *The Armyworm (Pseudaletia unipuncta (Haw.))*

a. Description, Injury, and Distribution. The young larvae of the armyworm are pale-green with alternate brown-to-reddish and light longitudinal stripes, which become more conspicuous in successive instars. The anterior prolegs of the first two instars are poorly developed.

In these stages the larvae are similar to measuring worms. Late-instar larvae vary in color from green to light-brown and red. The heads are pale-brown with a mottled area on each side of the median suture. When feeding in the corn ear, the mature larvae may easily be mistaken for the fall armyworm or the corn earworm.

The moths of the armyworm are brownish with a white spot near the center of the forewing. They are nocturnal in their flight habits but are attracted to lights in large numbers during outbreak years.

Injury on young corn is at first on the leaves and in the whorl; later the older larvae feed on the edge of leaves. The latter injury is common when migrations occur from small grains. A typical infestation shows plants with elongated lesions on and along the edge of leaves.

The armyworm is widely distributed over the United States and Canada as well as in foreign countries. Outbreaks are frequently local and sporadic, but high general populations have at times occurred over large sections of the eastern parts of the United States and Canada (Forbes, 1905; Walton and Packard, 1951).

b. Habits and Biology. The primary host plants of the armyworm are wheat, oats, barley, rye, and forage grasses. Forbes (1905) reported that armyworms pass the winter as partially grown larvae; this fact was confirmed by Davis and Satterthwait (1916) and Knight (1916). The overwintering larvae complete their development early in the spring and then burrow into the soil to pupate. The first brood of moths are abroad from April to June, depending on the bioclimate. They commonly deposit their eggs in beadlike clusters behind the sheaths and on leaves of small grain near the base of the plants. On hatching the larvae hide among the leaves during the day and feed on the upper leaves at night.

The presence of an infestation does not become conspicuous until the later instars, or about the time the heads of the grain appear. Migration to contiguous corn occurs from May to July, depending on the locality, under conditions of overpopulation and may extend a considerable distance into a field. Some infestations have been observed on early planted corn which resulted directly from first-brood oviposition. Forbes (1905) and Davis and Satterthwait (1916) estimated three complete generations in Illinois and Indiana, respectively. Knight (1916) observed two broods in New York. At about the roasting-ear stage of corn the larvae are not uncommon at the tip of the ear, causing injury similar to that of the corn earworm.

During an armyworm outbreak large numbers of larvae fall prey to parasites and predators. Knight (1916) recorded two species of tachinid flies, four of *Hymenoptera*, and five of predaceous beetles in

his observations in western New York. Among other predators the most common feeders are the blackbirds, sparrows, domestic fowls, skunks, and toads (Walton and Packard, 1951).

c. Chemical Control Measures. Because of the nocturnal feeding habits of the larvae, the early stages of an armyworm infestation are likely to escape observation. It is the late stages that are responsible for the spectacular sudden injury on small grains or grasses and the migration to contiguous corn. Chemical control practices should therefore be directed at the young larvae on the initial host. For many years poison-bran mash was the standard material for protecting crops against severe injury. Walton and Packard (1951) gave the following formula for an efficient bait: wheat bran 100 pounds, paris green or white arsenic 4 pounds, water 12 gallons. The mixture should be spread thinly over the field by hand or spreading machine, preferably late in the afternoon. As substitutes for the paris green or white arsenic Packard (1946) found calcium arsenate and sodium fluosilicate to be effective at 6 and 4 pounds per 100 pounds of bran, respectively. DDT dusts and sprays were relatively ineffective under conditions of his tests. In recent experiments toxaphene sprays have given promising results (Walton and Packard, 1951). Raun (1953) reported more than 99 per cent control from an aerial application of toxaphene at the rate of 2 pounds per acre on 250 acres of small grain.

6. Lesser Cornstalk Borer (*Elasmopalpus lignosellus*)

a. Description, Injury, and Distribution. The full-grown larva of the lesser cornstalk borer is about an inch in length, and greenish with conspicuous brown longitudinal stripes. The body color of the young larvae varies from pale-yellow to pale-green. The larvae have a distinctive habit of jerking and skipping when disturbed.

Typical injury in young plants is characterized by tunnels into the plant at or slightly below the surface of the soil. Heavy populations may cause loss of stand, stunting, and tillering. In older plants the injury in the stems is of a girdling nature near the ground, which makes plants more subject to stalk breakage. The presence of earthen silk-webbed tubes attached at the entrance of the tunnels indicates an infestation. These tubes are occupied by the larvae when they are not feeding in the plant (Luginbill and Ainslie, 1917).

The species is widely distributed over the warmer parts of North and South America. In addition to corn the more important crops attacked in the southern states are sugar cane, sorghum, cowpeas, and beans. Although the moths have been recorded in the more northern

states, infestations of economic importance have been reported only as far north as Arkansas (Isely and Miner, 1944).

b. Habits and Biology. According to Luginbill and Ainslie (1917), only the larvae survive the winter in their stalk burrows, and pupation and moth emergence take place in the late winter and early spring. At Columbia, South Carolina, the first-brood larvae on corn were nearly full-grown the first week of June. Information on the field biology and habits of the insect is incomplete. On the basis of rearing experiments they concluded that the insect developed four generations in that latitude. The records of outbreaks on various crops showed that infestations are most likely to occur under weedy conditions on sandy upland soils.

c. Cultural Practices. The cultural control practices suggested by Luginbill and Ainslie (1917) are aimed primarily at destroying the overwintering population through the elimination of crop debris by clean plowing in late fall or early winter. Early planting and fertilization are advocated as a means of producing vigorous growth and tolerance to an infestation. However, the effect of such practices in reducing the infestations in subsequent crops has not been evaluated. Isely and Miner (1944) reported that corn was the preferred host in an outbreak in Arkansas in 1943. This infestation followed heavy rains in May and June which resulted in abundant growth of crabgrass. Either the uninfested fields were cleaned up by cultivation or the weeds were destroyed by flooding. They concluded that clean cultivation before planting would prevent outbreaks of this insect.

7. Chinch Bug (*Blissus leucopterus* (Say))

a. Description, Injury, and Distribution. The adult chinch bug is about $\frac{1}{6}$ inch in length. It has a black, finely pubescent body with whitish wings. The wings have a triangular black area near the middle of the outer edge, and there is a triangular black scutellum between them at the anterior. The egg is reddish, elongate-oval, and about $\frac{1}{32}$ inch long. The nymphs are light-red at first, becoming darker red in each instar, until after the fourth molt they are practically black. Figure 18 shows a typical infestation of chinch bugs on a young plant (Forbes, 1905; Luginbill, 1922).

The chinch bug has been recorded from Central America and Mexico and is generally distributed over the United States and southern Canada. In some areas in the United States outbreaks have occurred periodically for more than 150 years. The most serious losses on corn have occurred in Ohio, Missouri, and the upper Mississippi Valley, Illinois being in about the center of the region of periodic outbreaks. Shelford and Flint (1943) made a study of the factors involved in the

fluctuation of chinch bug populations in the upper Mississippi Valley from 1823 to 1940. They concluded that population levels were correlated with meteorological conditions. Populations sufficient to cause crop damage were associated with above-normal temperatures and below-normal

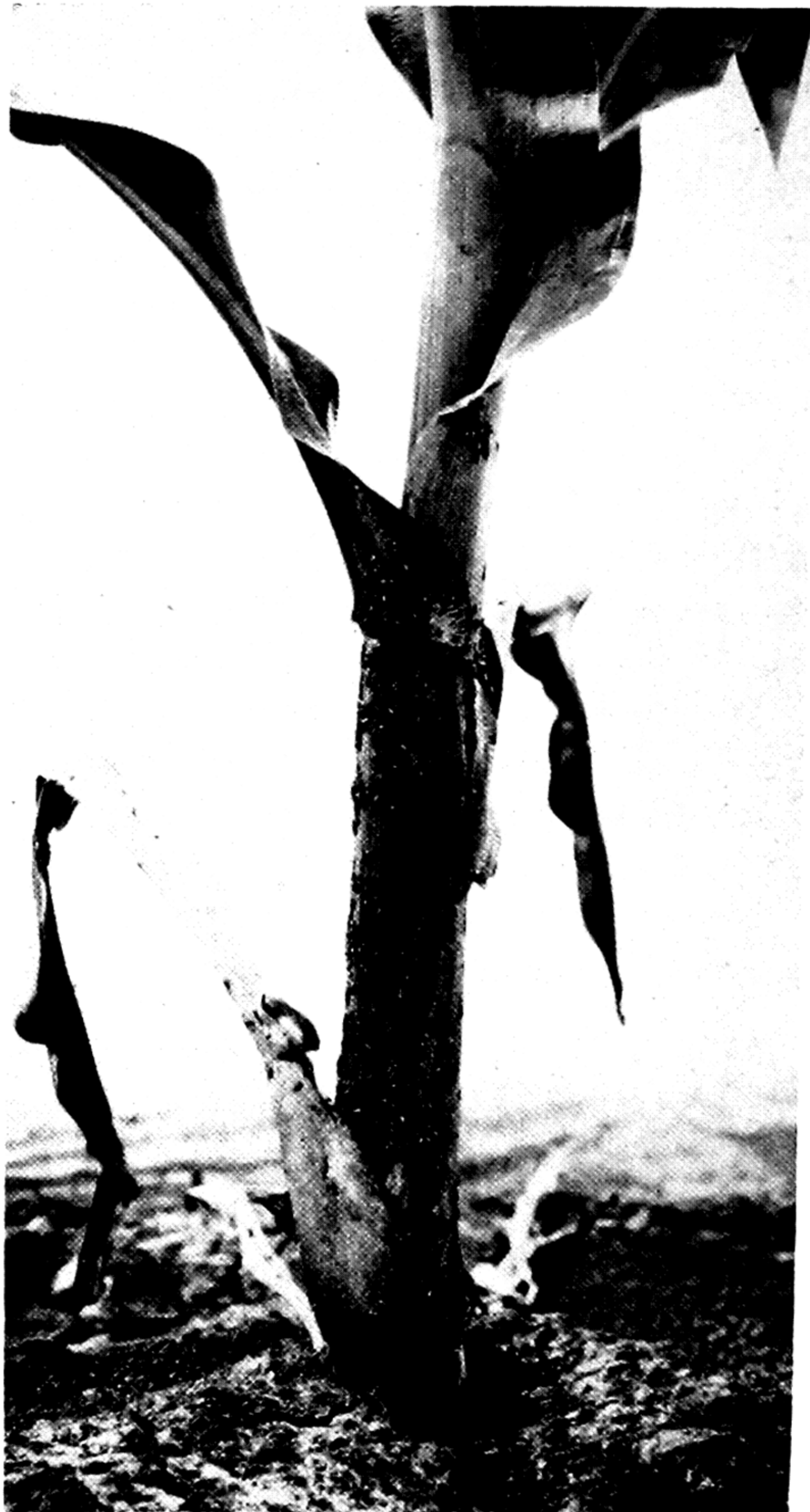


FIG. 18. Chinch bug infestation on young corn plant.

rainfall between March and October. No adverse effect could be attributed to below-normal winter temperatures.

b. Habits and Biology. So far as known the chinch bug feeds exclusively on plants belonging to the grass family. They attack wheat, barley, rye, oats, corn, and sorghum. The adults overwinter deep in clumps of sod of perennial grasses and in accumulations of leaves or

debris, concentrating in fence rows and southern or western exposure of wooded areas. They fly to such cover in the fall from corn, sorghum, or other hosts (Forbes, 1905; Headlee and McColloch, 1913). In the spring the bugs fly to the small grains. In Illinois Benton and Flint (1938) found wheat, rye, and barley most attractive to the bugs in the spring, and oats least attractive. The acreage of small grain was preponderantly in wheat and oats, and the latter occasionally had a heavy infestation. Early-planted corn may also be a host to the spring brood, especially in the Southwest.

The eggs are deposited around the base of the plants and behind the sheaths of the lower leaves, where they hatch in one to two weeks. The bugs obtain their food by sucking the sap from the plants, thereby causing serious injury to small grain under heavy infestations. Painter (1928), in a histological study of the tissues pierced by the sucking mouth parts of nymphs and adults, established that the stylets were thrust into the vascular bundles. He concluded that the food was obtained chiefly from the phloem and that feeding clogged the conductive tissue.

Small grains begin to ripen before much of the first brood reaches the adult stage. This condition results in the well-known on-the-foot migration from small-grain fields to adjoining corn, where the nymphs complete their development. The adults become abundant a few weeks later and distribute themselves by flight on corn, sorghum, or other grasses. The second-brood bugs complete their development on these crops in late summer and early fall. A third brood has been observed in the southern areas. The flight to their overwintering cover occurs in the late summer and fall, being heaviest at temperatures over 70°F. following cool nights. Among the important natural control agents that have been recorded are two fungus diseases, *Beauveria globulifera* and *Entomophthora aphidis*. A minute egg parasite, *Eumicrosoma benefica* Gah., is also considered to be of primary importance.

c. Cultural Practices. Various cropping practices have long been advocated when a chinch bug problem is threatened. The spectacular migration from small-grain fields to adjoining corn led to the recommendation to avoid planting corn next to small grain whenever possible. The cultural practices that produce good, vigorous stands of small grain and legumes have been observed to be unfavorable for the development of chinch bugs. It has been suggested that legumes be substituted for small grains in areas of heavy infestation.

d. Varietal Resistance. Flint (1921) reported the open-pollinated varieties CHAMPION, WHITE PEARL, and GOLDEN BEAUTY as resistant or tolerant to the attack of second-brood chinch bugs. In further tests in

Illinois Holbert *et al.* (1934) obtained data demonstrating that inbred lines resistant to second-brood bugs transmitted these qualities to top-, three-way, and double-cross hybrids. In a comparison of hybrids and open-pollinated varieties under an infestation of second-brood bugs, Holbert *et al.* (1935) found ILLINOIS HYBRID 391 to be superior in standing ability and yield. In tests under second- and third-brood infestations conducted in Kansas and Oklahoma, Painter *et al.* (1935) reported F₁ hybrids to have more resistance on the average than their inbred parents; this they thought to be due to one or both of two conditions, namely, specific inherited resistance and tolerance to, or escape from, injury associated with heterosis. They considered heterosis to be an important factor. Hybrids in general were superior to open-pollinated varieties, but a wide range of resistance was found in both groups. The pattern on corn appeared to be similar to that found on the sorghums.

e. Barriers and Chemical Control. Plowed furrow barriers with post-hole traps in the plowsole have been used for many years to protect corn from bugs migrating from small grain. Coal-tar creosote and dusts containing DDT or a dinitro compound make effective barriers, and creosote paper-fence barriers have been used effectively in reducing migrations into cornfields. Most of the creosote materials are repellent, whereas the dusts are toxic. Renewal of materials is dependent on weather conditions and the severity of the migrating populations (Decker, 1943; Packard *et al.*, 1950).

The most effective and practical chemical control method is of recent development. In tests conducted in Illinois Decker *et al.* (1953) and Bigger and Petty (1953) reported excellent results with dieldrin sprayed at the rate of 0.5 pound per acre as a barrier on a strip 2 rods wide in both the corn and small grain and on a similar strip across the ends and extending several rods into each field. In heavy migrations more than one application is advocated. All of the latest measures for chinch bug control are discussed in a recent publication (Anonymous, 1954b).

8. Grasshoppers (*Melanoplus spp.* and *Schistocerca americana* (Drury))¹

a. Description, Injury, and Distribution. Many species of grasshoppers attack corn and most other cultivated plants, but only a few of them cause serious crop losses. Of foremost importance on corn is the differential grasshopper (*Melanoplus differentialis* (Thos)). It is distinguished by its large size, 1½ inches in body length, and its dark-greenish or olive-brown color above to yellow underneath. This species

¹ The section on grasshoppers was prepared by R. L. Shotwell.

occurs abundantly in most of the eastern, midwestern, and Great Plains states south of the 47° parallel.

Of almost equal importance to corn is the two-striped grasshopper (*Melanoplus bivittatus* (Say)). This species is slightly smaller than *M. differentialis* and has two yellow stripes which extend back from the eyes along the sides of the thoracic shield to the tips of the tegminae. Elsewhere the body is generally olive-brown above to yellow underneath. *M. bivittatus* ranges over the entire United States and north into the Canadian provinces.

Of lesser importance on corn are the migratory and red-legged grasshoppers (*Melanoplus mexicanus* (Saus.) and *M. femur-rubrum* (Deg.)). These are of much the same size and general appearance, being about 1 inch long and reddish-brown to grayish above to greenish-yellow beneath, but the red-legged grasshopper has bright red hind tibiae. Both species are abundant throughout most of North America, being most injurious on small grains, clover, alfalfa, and pastures.

In the southern states the American grasshopper (*Schistocerca americana* (Drury)) is of some importance on corn. It is a large grasshopper 2 to 3 inches long and reddish-brown. When flushed these grasshoppers will rise quickly and make a long, wavering flight to some other resting place (Blatchley, 1920; Kuitert and Connin, 1952).

In 1931 the two species *M. differentialis* and *M. bivittatus* were responsible for the destruction of 25 to 75 per cent of all the crops destroyed by grasshoppers, including thousands of acres of corn in an area of 30,000 square miles in southern South Dakota and northeastern Nebraska. Again in 1936 they caused severe damage to corn in Iowa, Nebraska, Kansas, Missouri, and Oklahoma (Shotwell, 1941). Since 1929 *M. differentialis* has been the number-one corn-insect problem in south central South Dakota each year (Shotwell, 1949). In the great grasshopper outbreak of 1938 in the Dakotas, Nebraska, and Kansas, *M. mexicanus* was the dominant species and one of the most damaging to corn (Shotwell, 1939).

b. Habits and Biology. Eggs of these species are deposited some time during the late summer and early fall in pods 1 to 2 inches below the surface of the soil. The pods are 1 to 1½ inches long and contain 15 to 100 eggs per pod. *Melanoplus differentialis* and *M. bivittatus* concentrate their egg pods among the roots of weeds or grass along fence rows, roadsides, ditch banks, and other margins of cropped fields and pastures. Egg pods of *M. mexicanus* and *M. femur-rubrum* are deposited in the more open soil of small-grain stubble and bare spots in alfalfa and clover fields. *Schistocerca americana* deposits its pods in old weedy pastures, stump lands and abandoned lands common among

cropped fields in the South (Blatchley, 1920; Parker, 1930; and Shotwell, 1941).

The eggs of grasshoppers affecting corn hatch some time between April 1 and July 1, depending upon weather conditions and species. The young nymphs at first are less than $\frac{1}{4}$ inch long and grow to the adult stage by five to seven molts at intervals of four to eight days. Most of the injury to corn is done after midsummer by adults or nymphs in the last two stages which are migrating from adjacent small-grain and hay fields just harvested (Shotwell, 1941, 1949, 1952).



FIG. 19. Severe damage by grasshoppers.

Grasshoppers show a preference for corn silk and eat it down to the cob, destroying 25 to 60 per cent of the kernels. Often part of the cob is eaten. A population of 5 to 10 per square yard will do this much damage with little injury to the foliage. A greater number of 15 to 30 per square yard will chew the leaves to the midrib or cut them off at the axils, leaving nothing but the bare stalks (see Fig. 19). Still heavier infestations will eat waist-high corn stalks down into the ground, leaving the field bare of any corn plants (Shotwell, 1941).

c. Chemical Control Measures. Up to 1947 the use of poisoned bran-sawdust bait was the best-known method of control (Shotwell, 1942). It gave only partial and inconsistent protection to corn. From 1946 to 1953 extensive plot, field, farm, and community tests in several large agricultural areas proved that sprays or dusts containing chlordane, toxaphene, aldrin, dieldrin, or heptachlor practically eliminated the threat of grasshopper damage to corn and other crops (Shotwell, 1949, 1952; Kuitert and Connin, 1953; Parker, 1954). These insecticides are

now recommended for control of grasshoppers. Details on their formulations and proper use can be obtained from state agricultural experiment stations or the United States Department of Agriculture, Washington, D. C.

Corn at any stage of development can be sprayed from the air. Barriers of 10 rows of corn or 10 feet of weeds sprayed two or three times at four-day intervals will check grasshoppers migrating into the field and destroy the threat. One year's spraying on corn and other crops on some farms in South Dakota reduced grasshopper infestations to a point where no control was necessary for at least five years. They were farms on which grasshoppers had been an annual problem for 20 years (Shotwell, 1949, 1952).

9. *The Corn Leaf Aphid* (*Rhopalosiphum maidis* (Fitch))

a. Description, Injury, and Distribution. The corn leaf aphid is small, dark bluish-green, and wingless. Its colonies first become conspicuous on the top leaves and tassel tips as shown in Fig. 20. The winged form becomes abundant at about pollen shedding and silking time. Before tassel emergence the nymphal infestation occurs typically on the moist part of the leaves in the bud. In southern areas populations build up on small grains and wild grasses. In late winter and early spring they migrate to corn and sorghums as these crops approach the later whorl stages of growth. In more northern areas the infestations are sporadic with occasional years of high populations. When these infestations begin early in the season, considerable crop loss occurs as a result of varying degrees of barrenness. In warmer climates this aphid is a vector of some virus diseases. The species is world-wide in distribution.

b. Habits and Biology. The corn leaf aphid overwinters only in warm climates. Wildermuth and Walter (1932) reported corn, sorghum, and barley as preferred cultivated hosts and abundant populations on winter barley in the southwestern states. Forbes (1893) recognized the species as distinct from the corn root aphid and failed to find an oviparous generation or any winter survival of the viviparous forms in Illinois. The source of infestations in the northern areas is therefore believed to stem from a migrant population. The aphids appear in the central latitudes about the middle of July.

Both the winged and wingless forms produce living young, which under favorable conditions may build up to large colonies. The population usually reaches its maximum on the tassel just before the pollen is shed. In heavy infestations the extrusion of the anthers and pollen shedding may be considerably reduced. This is a common situation which every corn breeder readily recognizes in connection with con-

trolled pollination procedures. Moderate or heavy infestation on plants during the period of tassel emergence, pollen shedding, and early ear development results in an accumulation of carbohydrates in the leaves and abnormal synthesis of anthocyanin and reddening of the leaves. Poor seed set is therefore a common reaction from aphid attack (Forbes, 1893; McCollock, 1921; Wildermuth and Walter, 1932).



FIG. 20. Leaf and tassel infestation by the corn leaf aphid.

Extremes of temperature are unfavorable for aphid development. The aphids seem to reach their maximum reproductive capacity in periods of cool temperatures which are unfavorable for some of their important predators and parasites. Wildermuth and Walter (1932) observed this relationship in the southwestern states, and Walter and Brunson (1940) reported similar observations in Indiana. *Lysiphlebus testaceipes* Cres., a small hymenopterous parasite, the common lady beetles *Hippodamia convergens* Guir. and *Coleomegilla maculata*

(Deg.), and the lacewing flies are the dominant natural enemies (Wildermuth and Walter, 1932).

c. Varietal Resistance. Differences in varietal response to the corn leaf aphid have been recorded by several workers. McColloch (1921) reported differences between open-pollinated varieties. He observed that there was a tendency for the later maturing varieties to be most heavily infested. Walter and Brunson (1940) tested a large number of inbred lines and hybrid combinations and found no plant characters that could be consistently correlated with resistance, although a large proportion of the inbreds and hybrids with a large and compact tassel were attractive to aphids. With some exception, hybrids were less heavily infested than the parental lines. These workers reported practical immunity for the inbred lines R4 and YS79, and found the lines 38-11 and CI.4-8 to be extremely susceptible.

Snelling *et al.* (1940) expressed the opinion that the best promise for the control of the corn leaf aphid was in the development and utilization of resistant strains. They tested a large number of lines at different places in Illinois. Little barrenness was observed in plants with no infestation, whereas in aphid-infested plants there was a high rate of barrenness. Huber and Stringfield (1942) presented data showing a correlation between resistance to corn leaf aphid and the European corn borer in a group of lines tested in single-cross combinations. Coon *et al.* (1948) found a significant correlation between the carotene content of the seed and the degree of aphid infestation, the high carotene parent lines being the more susceptible, although individual lines were variable. Such correlations depend on the reactions of the lines under test. When tests are unbalanced with lines that are variable in resistance factors for both insects, the correlation may be poor or negative.

10. *The Corn Flea Beetle (Chaetocnema pulicaria Melsh.)*

a. Description, Injury, and Distribution. The adult is the primary injurious form of the corn flea beetle. It is oblong, very dark, shiny green, and about $\frac{1}{16}$ inch long. The feeding lesions on the leaves form a pattern of narrow closely spaced lines which normally run parallel with the veins. The lesions are about $\frac{1}{4}$ inch in length. They are points of origin of Stewart's bacterial wilt, which in its more advanced stages may obscure the beetle lesions in susceptible varieties. The role of this beetle as a vector of the disease is discussed in Chapter XII. (See also Rand and Cash, 1933; and Poos and Elliott, 1936.)

The corn flea beetle is widely distributed over the eastern and central parts of the United States. Large populations occur periodically in these regions, where infestations on field and sweet corn are sometimes

severe. Forbes (1905), in discussing the importance of this insect in several states, indicated that wilting was associated with the injury and that the beetles were especially fond of sweet corn.

Other species of flea beetles are commonly found on corn and cause similar injury. The toothed flea beetle (*Chaetocnema denticulata* (Ill.)), which is metallic green and about twice as large as *C. pulicaria*, is more closely associated with the wild grasses that persist in cornfields. This species is also capable of transmitting Stewart's disease, but with less virulence (Poos and Elliott, 1936; Elliott and Poos, 1940). In the southwestern states the desert corn flea beetle (*C. ectypa* Horn) is generally distributed as a pest of corn (Wildermuth, 1917). Evidence of its ability to harbor and transmit Stewart's disease has not been established.

b. Habits and Biology. The adults of the corn flea beetle feed on many plants. Forbes (1905) and Elliott and Poos (1940) list a wide host range, but the cereal and forage grasses, wheat, oats, barley, rye, bluegrass, timothy, and orchardgrass, are probably the most important. There is little published information on the habits and biology of the insect in its soil environment. F. W. Poos, of the Entomology Research Branch of the United States Department of Agriculture, who for several years investigated the biology of the species and its transmission of Stewart's disease, kindly made available the following summary of his results:

The biology of this insect was studied at intervals during the period 1934-41, mostly as a vector of Stewart's disease or bacterial wilt of corn in the vicinity of Washington, D. C. The insect was found to overwinter as an adult, mostly in the top inch of the soil and primarily in bluegrass sod. On days when the air temperature near the surface of the soil reached 67-70°F. for a period of a few hours, the adults became active during the winter. The longer the temperature remained above 65° the more numerous the adults became, until in late spring they became generally dispersed. New broods of adults were observed at various times during the season. Emergence of a brood was concentrated after a good rainfall following dry soil conditions. This was observed as early as June 9 and as late as August 8, making it evident that at least two complete generations of this insect occurred each season.

The average number of days required for the development of the different stages under laboratory and greenhouse conditions were as follows: egg incubation 5.8; larval 15.5; prepupal 2.1; pupal 5.3. The period from egg to adult of 33 individuals ranged from 22 to 36 days and averaged 29.7 days.

By washing the soil, taken under isolated plants, in water to which 6 to 12 percent Epsom salts was added to aid in floating out the very small larvae, this insect was found developing on 21 species of grains and grasses including corn (both field and sweet), barley, oats, wheat, orchardgrass, timothy, red top, and Italian ryegrass. Larvae would not feed on alfalfa and adults lived only about 10 days when confined to this host plant. Evidence was obtained indicating that a generation developed on wheat and timothy in 1940 before corn was generally available in the field.

c. Chemical Control Measures. The means of protecting corn from Stewart's disease has been through the use of resistant strains. This method has met with success and is one of the important considerations in the development of sweet corn inbreds. Under severe beetle infestation on young corn direct control by insecticides is warranted. Poos (1945) showed that several applications of a 0.66 per cent DDT suspension spray containing a spreader and resinous sticker gave protection against a moderate infestation of beetles on three varieties of sweet corn which varied in resistance and susceptibility to wilt. Treated rows had better stands than untreated rows and the plants were taller, particularly in the wilt-susceptible variety. His observations indicated that Stewart's disease had some dwarfing effect on the wilt-resistant variety, even though there were no external symptoms of the disease.

11. Japanese Beetle (*Popillia japonica* Newm.)

a. Description, Injury, and Distribution. The injurious form of the Japanese beetle on corn is the adult. It is about $\frac{1}{2}$ inch long, oval, with a metallic green body and brownish wing covers. The beetle can readily be identified by the six conspicuous tufts of white hair along the outer edge of each wing cover. Typical injury is scatter-grain, particularly at the tip of the ear, due to feeding on emerging silks. As a pest of corn this beetle is most important in the Middle Atlantic and southern New England states (Hadley and Hawley, 1934).

b. Habits and Biology. The beetles emerge in June and July, and there is but one brood annually. Egg deposition is predominantly in grass sod. On hatching the larvae feed on fine plant roots and organic matter in the soil until fall and again in the spring. Pupation occurs in May and early June. Favorable situations for the development of larvae are lawns or short grass pastures. The adults feed on many species of plants, corn in the silking stage being one of the preferred hosts. The beetles have a gregarious feeding habit, and when they concentrate on the emerging silks, pollination and seed set is interfered with to varying degrees. The scatter-grain is therefore the result of continued attack and shearing of emerging silk (Hawley and Metzger, 1940).

c. Varietal Resistance. Differential attractiveness has been observed in experimental tests of different strains of corn. Coon (1951) reported that this differential effect decreases as the population of beetles increases, disappearing when 50 per cent or more of the silks are removed from 80 to 100 per cent of the ears. He states that little damage may result even though silks have been heavily denuded. Some of the factors involved in the extent of injury are silking date, level of beetle

populations, abundance and duration of pollen flow, rate of silk growth, and rapidity of pollen grain germination and growth after adherence to the silk.

d. Chemical Control Measures. Protection against beetle injury on corn can be obtained by applying DDT dust (Coon, 1951).

V. Lesser Recognized Groups

a. Thrips. Although several species of thrips are almost invariably present on corn, particularly in its early stages of growth, very little is known about their effect on plant growth. The writer has observed high populations of the grass thrips (*Anaphothrips obscurus* (Müll.)) and lesser populations of *Frankliniella tenuicornis* (Azal) in northern Ohio. Thrips injury is characterized by a silvery mottled appearance of the lower leaves which is sometimes more intense along the edges of the leaves. The young larvae are primarily located in the moist rolled leaves of the bud, whereas the adults commonly occur under the fully exposed leaves. Differential feeding on inbred lines of corn has been pronounced under a high level of infestation. Elliot and Poos (1940) reported on tests with *A. obscurus*, *Aeolothrips fasciatus* (L.), and *Hercino femoralis* (Reuter) as possible vectors of bacterial wilt. A single isolation was obtained from *A. obscurus*.

b. Leafhoppers. Many species of leafhoppers have been recorded on corn. Neiswander (1926) lists 59 species. The significance of the injury caused by most of these species is not well established. The lantern fly (*Peregrinus maidis* Ashmead) is a pest of corn in tropical and semi-tropical areas. This species concentrates its feeding on the bud leaves. It is a proved vector of mosaic virus (see Chapter XII). Leafhoppers are nearly always abundant on small grain and pasture grasses. Some of the same species commonly occur on corn. Others are vectors of virus diseases and are discussed under that subject. A pale-green mirid, *Trigionotylus brevipes*, Jakovlev, feeding on the leaf blades was observed by the writer to be abundant on mid-whorl stages of growth for several years in northern Ohio.

VI. Insects in Relation to Diseases of Corn

The transmission and dissemination of pathogenic organisms and viruses on corn by insects have been investigated over a period of years. An important phase of this study of insects as vectors is the overwintering source of the causal agent. Leafhoppers and aphids are probably the most important vectors. A discussion of the literature on insects as vectors of plant diseases in cereal and forage crops was published by

Poos (1938). Additional information has accumulated on some diseases and their vectors since his review.

a. Fungus Diseases. The microorganisms associated with the rots that develop in the stalk and ear following infestation by the European corn borer were investigated in Minnesota by Christensen and Schneider (1950). Species of *Fusarium* were the most common pathogens isolated from injured points in the stalk, shank, and ear. During the summer and fall the larvae of the corn borer harbored stalk rot organisms both externally and internally. On sweet corn Pepper and Haenseler (1944) observed less smut where the European corn borer was controlled with insecticides, indicating that the organisms gained entrance to the plant at the point of borer injury.

Fungus infections are usually associated with damage to the ear caused by the corn earworm. Koehler (1942) reported that corn ear rot due to *Fusarium moniliforme* is increased by corn earworm damage. He found that kernel infections of this rot were similarly increased most by earworm damage. Next in order of increase were *Gibberella zeae*, *Nigrospora* spp., and *Cephalosporium acremonium*, but the last two were increased slightly. *Diploidia zea* infection was not affected by earworm injury.

b. Bacterial Diseases. Stewart's disease, caused by *Aplanobacter stewartii*, is a bacterial wilt of sweet corn and occasionally is of importance on field corn. The relation of insects to this disease was discussed by Rand and Cash (1933). They reported that (*Chaetocnema pulicaria* Melsh.) the corn flea beetle, the toothed flea beetle (*C. denticulata* Ill.), and the southern corn rootworm beetle (*Diabrotica undecimpunctata howardi*, Barber), were able to disseminate the disease when they were transferred from diseased to healthy corn plants under caged conditions.

The importance of the corn flea beetle in the incidence of this disease was further reported by Elliott and Poos (1934), particularly in connection with the overwintering of the disease organism. They found that at least 19 per cent of the overwintered beetles carried the disease organism. From tests of about 40 species of insects as possible vectors of Stewart's disease, Poos and Elliott (1936) concluded that only *Chaetocnema pulicaria* and *C. denticulata* were vectors under field conditions. From May to September in 1934 they found 40 per cent of *C. pulicaria* harboring the organism. *Diabrotica undecimpunctata howardi* transferred wilt organism from diseased to healthy corn under experimental conditions. A correlation between winter temperatures and the abundance of the corn flea beetle and the incidence of Stewart's disease was indicated in New York and New England in 1934. The

corn flea beetle was not abundant north of central Pennsylvania in 1934, and Stewart's disease was much reduced below the levels which prevailed in 1932 and 1933.

c. Virus Disease. Several virus diseases transmitted by insects have been investigated since Brandes (1920) reported the transmission of the sugar-cane mosaic virus to corn by *Aphis maidis* Fitch. All of these viruses are transmitted by leafhoppers or aphids.

Kunkel (1921) reported *Peregrinus maidis* Ashm. as a possible vector of corn mosaic in Hawaii. This species was further investigated by Carter (1941), who confirmed Kunkel's work and found that the incubation period usually varied from 11 to 29 days, and in rare instances was as short as 4 days. The virus persisted in the insect and in most cases was transmitted without interruption when 2-day feeding periods were used.

The incidence of mosaic on corn in the presence of *A. maidis* was also reported by Knechtel and Manolache (1944) in Rumania.

The transmission of the streak disease of maize in South Africa by the leafhopper *Cicadulina mbila* (Naudé) was studied by Storey (1925). He was unable to transmit the disease by other means of inoculation. Storey (1939) summarized his studies on the transmission of viruses in maize by *Cicadulina* spp. He found the corn streak virus to be transmitted when the leafhopper pierced the phloem during feeding. His work showed that variability of *C. mbila* (Naudé) to become infective occurred in field populations and that overwintering viruliferous adults were the source of infection in early-planted corn in the spring. By selective breeding he segregated races of the leafhopper according to their ability to transmit the virus, designating them as active and inactive races. In crosses among strains of leafhoppers activity was found to be dominant to inactivity. The inheritance of the ability to transmit the virus was determined to be a simple dominant Mendelian sex-linked factor. He found that an inactive race could be made active by puncturing the stomach, and thus showed that there was no diffusion of the virus through the tissues of the stomach wall in the inactive forms.

Storey (1937) described the "mottle" disease in Tanganyika Territory, Africa, and was able to transmit it with two newly described leafhoppers, *Cicadulina dipunctella* Mats. and *storeyi* China, and also with the vector of the streak disease, *C. mbila*. Mechanical inoculation was unsuccessful. In Florida, Wellman (1934) reported the transmission of celery mosaic, a strain of the cucumber mosaic virus, by *Aphis gossypii* Glov. from celery and *Commelina nudiflora* to dent, flint, and sweet corn, and to popcorn.

The transmission of stunt disease of corn, which occurs in Texas and California, by the leafhopper *Baldulus maidis* (Del. & Wolcott) was first reported by Kunkel (1946). He was able to maintain a non-viruliferous population of *B. maidis* by isolating newly hatched nymphs before feeding and rearing them on disease-free corn. The leafhoppers that developed on diseased corn became viruliferous. Transmission by mechanical means and transmission by dodder were unsuccessful. In further studies of corn stunt (Kunkel, 1948), leafhoppers, transferred daily to healthy plants, remained viruliferous as long as 88 days after a 1-day exposure on diseased plants. Both nymphs and adults transmitted the disease. Transmission tests with the aster leafhopper (*Macrosteles divisus* (Uhler)), and *Peregrinus maidis* (Ashm.) gave negative results. The transmission of corn stunt by *Baldulus elimatus* (Del & Wolcott), a leafhopper common on corn, was reported by Niederhauser and Cervantes (1950).

A new aphid-borne virus disease of corn was described from California by Stoner (1952) and named "leaf fleck." Transmission tests with *Rhopalosiphum prunifolae* (Fitch), *R. maidis* (Fitch), and *Myzus persicae* (Sulzer) gave positive reactions. Transmission through the soil and transmission by mechanical means were unsuccessful. *R. prunifolae* in daily transference experiments remained viruliferous throughout its life.

VII. Stored-Grain Insects

The most injurious insects found in stored corn also infest other grains, cereal products, and stored food or feed. The problems of controlling these insects on corn are frequently related to problems of their control on other grains and products. Cotton *et al.* (1953) have brought together the significant information on the causes of outbreaks of stored-grain insects. This information applies chiefly to the grain-producing region of the North Central States, but much of it also applies to other regions. Stored-grain insect infestations in corn are most intense in warm climates, where the problem begins in the field and continues on through the storage period. Some of the more general information on the most important species encountered in corn storage is summarized below.

1. The Rice Weevil (*Sitophilus oryza* (L.))

a. Description, Injury, and Distribution. The rice weevil is a dark reddish-brown snout beetle, about $\frac{1}{6}$ inch long, with two light spots on each wing cover (Fig. 21A). The thorax is densely pitted, the legs

are prominent, and the wings are well developed. The larva, which feeds in the grain, is a white, legless, thick-bodied grub.

The rice weevil has a wide range of hosts among the grains in storage and in warm climates also in the field. In the lower Temperate Zone and in the Tropics it is one of the most important economic insects. In the United States infestations extend into the southern part of the North Central States following mild winters. In the South it is by far the worst insect pest of stored corn. The primary source of infestations in the North is the transportation of infested grain or small cultures located in favorable spots for surviving the winter (Dean, 1913; Cotton, 1920).

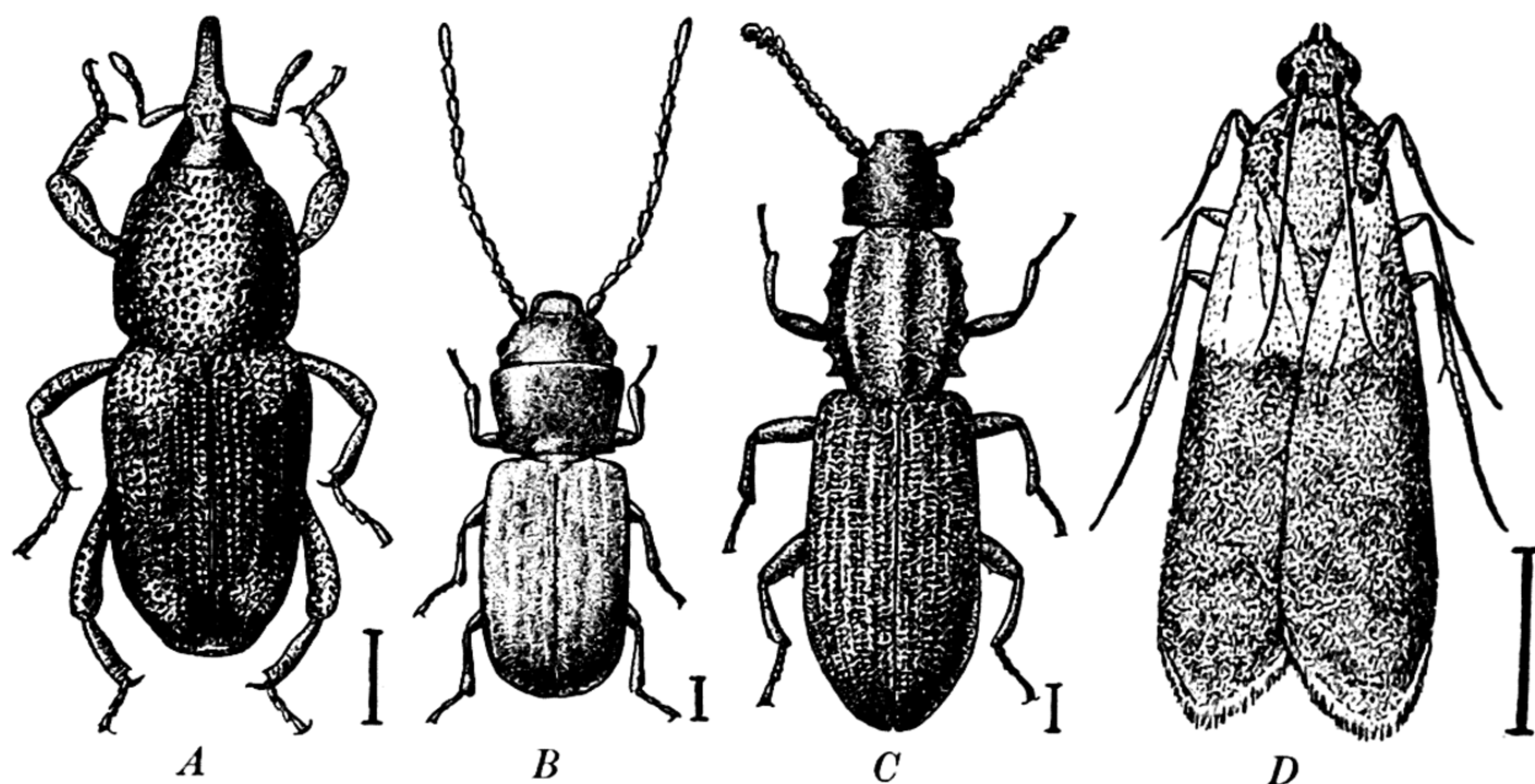


FIG. 21. Left to right: Adults of rice weevil; flat grain beetle; saw-toothed grain beetle; Indian-meal moth. (Courtesy of the Iowa Agricultural Experiment Station.)

b. Habits and Biology. The adults of this beetle eat small cavities in the grain in which to deposit their eggs. Under favorable temperature and humidity, egg deposition by an individual may extend over four or five months. On hatching the larvae feed in the grain on both germ and endosperm. Pupation takes place in the grain in the cavity made by the larva during its feeding. During the summer months about 35 days are required to complete a generation (Cotton, 1920). There may be seven generations annually in the South, but not so many in the North.

The fact that the beetles are strong fliers is important in the dissemination and establishment of field infestations in areas where there is normally an overwinter survival in stored grain. Cotton (1920) observed that the infestations in corn in the field began after the grain became firm. A relationship between husk protection and injury by the corn earworm and rice weevil in the field and in storage was reported by Hinds (1914), Kyle (1918), Cotton (1920), and Cartwright (1930).

c. Varietal Resistance. The possibilities of developing strains of corn that would give good protection against the corn earworm and the rice weevil were pointed out by Kyle (1918). The corn-development programs have emphasized this approach in recent years in areas where the rice weevil is a chronic pest in storage and in the field. Eden (1952) confirmed that rice weevil injury decreased as the husk extension and layers increased, but observed that the effects of the two characters were independent. In tests of kernel hardness in 20 varieties and hybrids adjusted to 12 per cent moisture, he calculated that there was a 1 per cent decrease in damage for each pound of pressure per square inch required to penetrate the kernels with a $\frac{1}{16}$ -inch hollow punch. A variation in pericarp thickness was not correlated with the amount of damage.

d. Chemical Control Measures. Douglas and Smith (1953) reported almost complete absence of the rice weevil in ear corn until harvest in November in Louisiana tests where they had practically eliminated the corn earworm and fall armyworm with a DDT-mineral oil emulsion spray. The control of the earworm and the fall armyworm with insecticides has been discussed on pages 564 and 574.

2. *The Granary Weevil (Sitophilus granarius (L.))*

a. Description, Injury, and Distribution. The granary weevil is closely related to the rice weevil and may be easily confused with it. The light spots on the wing covers, typical of the rice weevil, are lacking, and the wings are reduced to a vestige. The larva inhabits the grain in a manner similar to that of the rice weevil. It has a wide host range among cereal grains and products, in which it has become a cosmopolitan pest (Dean, 1913).

b. Habits and Biology. The granary weevil has a life history similar to that of the rice weevil, but it is not as widespread a pest of stored corn. It is more tolerant of cold climates (Decker, 1941) and is not considered a serious pest of corn stored in the South. In Kansas Dean (1913) has reported four or five broods annually. Because of their inability to fly the beetles become disseminated only through the transport of grain and other infested products stored under favorable conditions.

3. *The Flat Grain Beetle (Laemophloeus pusillus (Schönk.))*

a. Description, Injury, and Importance. The flat grain beetle is a reddish-brown beetle, about $\frac{1}{16}$ inch long, with long antennae extending somewhat in a V-shape from the head. The adults feed mostly on grain dust or broken kernels, whereas the larvae like to burrow into

the germ. See Fig. 21B. In recent years this species has been present in large numbers in out-of-condition corn in storage. Infestations show grain with the germ eaten out and association with primary infestations by the rice weevil and the cadelle (Cotton, 1947; Cotton *et al.*, 1953).

b. Habits and Biology. The flat grain beetle is attracted to, and breeds in, grain that is in poor condition. Decker (1941) and Cotton *et al.* (1953) report the species as among the most abundant in shelled corn stored in steel bins, but it has not been regarded as a serious pest in sound corn. A closely related species, *Laemophloeus ferrugineus* (Steph.), is similar to it in appearance and habits, and according to Cotton (1947) is more resistant to cold weather and more commonly found in stored grain in northern states.

4. Saw-Toothed Grain Beetle (*Oryzaephilus surinamensis* (L.))

a. Description, Injury, and Distribution. The saw-toothed grain beetle is readily indentified by the six tooth-like projections on each side of the thorax. These also occur on the pupa. It is dark brown and about $\frac{1}{10}$ inch long. See Fig. 21C. The larva is slender and yellowish-white. Both adults and larvae are free feeders in grain, injuring more seeds than they consume. The species is world-wide in distribution and infests a great many grains, seeds, and foodstuffs. This beetle and the flat grain beetle are the two most abundant of insect pests in shelled corn.

b. Habits and Biology. The adults are long-lived but the immature forms develop in about three weeks under favorable conditions. The egg deposition period ranges from 6 to 10 months, according to Back and Cotton (1926). On completing development, the larva transforms into a pupa in a light cocoon bound together with foodstuff fragments. Because of the variable length of adult life it is difficult to determine the number of generations. In the vicinity of Washington, D. C., Back and Cotton (1926) estimated from four to five generations and believed breeding to be continuous in subtropical and tropical climates. The winter is passed in the adult stage. Under low humidity in heated buildings development of larvae is much inhibited.

5. The Cadelle (*Tenebroides mauritanicus* (L.))

a. Description, Injury, and Distribution. The cadelle is one of the largest of the common stored-grain pests. The adult is dark reddish-brown, oblong, flat, and about $\frac{1}{3}$ inch long, with a conspicuous constriction just ahead of the wings. The mature larva is about $\frac{3}{4}$ inch long, white, with a black head and two caudal spines. The head and

thoracic segments are narrower than the abdominal segments. Both adults and larvae prefer the germ for food.

The larva has a habit of burrowing into wooden structures before pupation; this is an important factor in control practices in some areas. Other grain insects usually follow up its attack. The species is world-wide in distribution. It has a wide host range among grains and stored products (Back and Cotton, 1926). It is not abundant in shelled corn stored in steel bins.

b. Habits and Biology. Among the important stored-grain insects the cadelle is probably the most hardy under winter temperatures in the more northern corn-growing areas. The overwintering population is made up of both adults and larvae. The infestations in the spring result from the beetles and larvae that survive the winter. Back and Cotton (1926) reported oviposition throughout the spring and summer months. The number of generations could not be determined. Continuous breeding occurs in warm climates.

6. *The Flour Beetles (Tribolium spp.)*

a. Description, Injury, and Distribution. The flour beetles are flat, reddish-brown, and about $\frac{1}{6}$ inch long. The larvae are about $\frac{1}{4}$ inch long when full grown and have a forked termination of the last abdominal segment. Although they are usually associated with flour and meal storage, they are commonly found in stored corn. Like the other stored-product insects, they are world-wide in distribution and thrive on a large variety of seeds and food products. The most common species are *Tribolium castaneum* (Hbst.) and *T. confusum* Duv. (Good, 1936). In late summer *T. castaneum* (Hbst.) often becomes exceedingly abundant in shelled corn stored in the commercial corn area.

b. Habits and Biology. Both adults and larvae feed on stored corn, but prefer broken kernels. Because they shun light they are seldom noticed when low populations are present. The adults are long-lived, but the immature stages are short. The oviposition period may extend for a year. The number of generations produced annually depends on the bioclimate. Continuous breeding is believed to occur in the Gulf states, but only in heated buildings in the extreme northern states and Canada. Dissemination by flight for a short distance is considered possible only for *Tribolium castaneum* (Hbst.). For this reason this species is the predominant one in farm stored grain.

7. *Angoumois Grain Moth (Sitotroga cerealella (Oliv.))*

a. Description, Injury, and Distribution. The injurious form of the Angoumois grain moth is a small white caterpillar with yellowish head

which feeds within the grain. Pupation occurs in the cavity hollowed out by the larva. Typical indications of an infestation are kernels with round holes or with small channels stopping just below the seed coat and the presence of buff-colored moths with pointed hair-fringed wings measuring about $\frac{1}{2}$ inch when spread.

As a pest of grain the Angoumois grain moth is next to the rice weevil in economic importance. It is distributed throughout the world, infesting grain in storage and in the field in the lower Temperate Zone and the Tropics. It is most damaging to corn in the southern part of the North Central States. It occurs in outbreak numbers in this region only after a series of warm winters have allowed populations to build up. In bad years it is not uncommon to find as many as 10 per cent of the kernels infested. In the South it is never as troublesome in corn as the rice weevil (Simmons and Ellington, 1933; Cotton *et al.*, 1953).

b. Habits and Biology. In the areas where the Angoumois grain moth is a pest, corn serves as an important source for building up infestations in other grains, particularly in the field and in storage. As with the rice weevil, corn becomes infested in the field, the ears with exposed tips being most susceptible to attack. In the South there is a continuing infestation in cribbed corn. In stored shelled corn the infestation is concentrated near the top of the bin. Simmons and Ellington (1933) reported on the life history and host activity of the insect in Maryland. In that area they observed winter survival primarily as full-grown larvae in grain in storage and in straw piles, baled straw, and litter. Light infestations were present in corn with exposed ear tips at harvest-time. Cartwright (1930) showed an inverse relationship between damage and husk extension beyond the ear.

8. Indian-Meal Moth (*Plodia interpunctella* (AbN.))

a. Description, Injury, and Distribution. The full-grown larvae of the Indian-meal moth are about $\frac{1}{2}$ inch long and vary in color from whitish to green or pink. When at rest the moths are easily recognized by their brown color and a light transverse band on the forepart of the wings. See Fig. 21D. In typical injury the embryo of the corn kernel is devoured, and silken webs are spun over the infested grain or meal. It breeds in ear, shelled, and ground corn and on a wide variety of grains and cereal products. It is widely distributed in grain-growing countries (Dean, 1913).

b. Habits and Biology. In the South breeding in ear corn is continuous through most of the year. In the North Central States the moths fly to the bins of shelled corn in midsummer and lay their eggs on the surface grain. In some years this insect is so abundant that the entire

surface of the bins is covered with a silky webbing and hordes of larvae may be seen crawling over the outside walls. Dean (1913) estimated the number of generations produced annually to be from four to seven, depending on temperatures.

9. Pink Corn Worm (*Pyroderces rileyi* (Wlshm.))

a. Description, Injury, and Distribution. The injurious form of the pink corn worm is a pink or rose-colored larva about $\frac{3}{8}$ inch long when full grown, which begins its infestation on the ear in the field and continues to feed on the corn in storage. The moth has mottled yellow, brown, and black forewings and long-fringed narrow hindwings. It is smaller than the Angoumois grain moth, with which its populations may be mixed. In typical injury the ear is webbed with frass, which is filled in between the rows of grain and in the larval cavities. The injury and the silk webbing are not unlike those of the Indian-meal moth. The species is tropical and subtropical in distribution and is a pest of corn, sorghum, and cotton in the South Atlantic and Gulf states (Chittenden, 1916).

b. Habits and Biology. According to Chittenden (1916), the pink corn worm infests corn in the field that has been infested with earworms or has had the husk cover broken in some other way. He observed ears infested about at the milk stage or a little later. Breeding is continuous through the fall and after harvest in storage, most complaints coming in November and December. The larvae feed also on the husk and cob but have a habit of feeding in the grain on the embryo and the endosperm.

10. Other Insects

The foreign grain beetle (*Ahasverus advena* (Waltl.)), the hairy fungus beetle (*Typhaea stercorea* L.), and the larger black flour beetle (*Cybaeus angustus* (Lec.)), are often abundant in shelled corn stored in the North Central States. They are attracted to corn that is slightly out of condition but seldom cause appreciable damage to corn in good condition.

11. Control of Stored-Grain Insects

The practices recommended for controlling insects in stored corn vary with the environmental conditions under which the crop is produced, the handling of the crop, the storage facilities, and the species present. Temperature and moisture are the most important environmental factors.

Cotton (1938) has evaluated the storage problems in four general regions. In region 1, which comprises the northern corn-growing areas,

crib-stored corn is free of these pests over winter. In shelled corn the sources of infestation are old grain and feed situated in places favorable for winter survival. Farm storage is considered to be relatively safe. In region 2, the central part of the commercial corn-growing area; monthly inspections of grain during the warm months are advised. In region 3, which includes a zone from Pennsylvania to Virginia and the southern part of the North Central States, grain corn storage becomes more hazardous because of more favorable conditions for winter survival. In the southern part of this region field infestations of the Angoumois grain moth and rice weevil, beginning in wheat before harvest and continuing in corn later in the season, make crib and bin storage on the farm hazardous; monthly inspections except in the winter are advised. In the southern corn-growing areas, designated as region 4, conditions are favorable for the development and winter survival of storage pests. Field and storage infestations are chronic under farm conditions. Immediate fumigation when grain is placed in storage and monthly inspection for possible refumigation is essential in this region.

a. Control Practices. Systematic application of preventive measures and fumigation are effective in keeping stored-grain pests in check. For regions 1, 2, and 3, Cotton *et al.* (1953) summarize these practices for farm-stored grain as follows:

Store only dry grain (12 percent moisture or less); store in weather-tight, rodent-proof bins, preferably of steel; clean out all bins before loading with grain; spray walls and floors of bins and adjacent woodwork of farm buildings with a residual type spray; clean up and dispose of litter, waste grain, and feed that have accumulated in and around farm buildings; fumigate two to four weeks after placing small grains and shelled corn in storage; inspect frequently and refumigate if an infestation is discovered. Small grains can be treated before binning with grain protectants in lieu of fumigation.

For shelled corn in farm bins the fumigants recommended are carbon tetrachloride alone, or 4 parts of carbon tetrachloride to 1 part of carbon disulfide applied at the rate of 6 gal. per 1000 bu.; or 1 part of carbon tetrachloride to 3 parts of ethylene dichloride applied at 8 gal. per 1000 bu. For a surface protection especially against the Angoumois grain moth and the Indian-meal moth they recommend a refined white oil of 100 to 200 seconds viscosity (Saybolt at 100°F.) sprayed at the rate of 2 quarts per 100 square feet of surface.

Acknowledgment

The writer has consulted freely with other workers who are interested in various phases of research on corn insects. Grateful acknowledgment for helpful advice or assistance is made to the following persons: J. W. Ingram, T. A. Brindley (also of

Iowa State College), G. F. Sprague, A. M. Vance, and H. C. Cox of the Agricultural Research Service and H. H. Walkden of the Agricultural Marketing Service, United States Department of Agriculture, and J. H. Lilly and H. C. Gunderson of the Iowa Agricultural Experiment Station.

REFERENCES

- AINSLIE, G. G. 1919. The larger corn stalk-borer. *U. S. Dept. Agr. Farmers' Bull.* **1025**.
- AINSLIE, G. G. 1922. Webworms injurious to cereal and forage crops and their control. *U. S. Dept. Agr. Farmers' Bull.* **1258**.
- AINSLIE, G. G. 1927. The larger sod webworm. *U. S. Dept. Agr. Tech. Bull.* **31**.
- ANONYMOUS. 1937-1938. *Ohio Agr. Expt. Sta. Ann. Rept. Bull.* **600**: 26-27.
- ANONYMOUS. 1952. The European corn borer and its control in the north central states. *North Central Regional Publ.* (Revised) **22**. *Iowa State College Pamphlet* **176**.
- ANONYMOUS. 1954a. Chinch bugs and how to control them. Entomology Research Branch. *U. S. Dept. Agr. Leaflet* **364**.
- ANONYMOUS. 1954b. The sugarcane beetle on corn in the Southern States. Entomology Research Branch, Section of Cereal and Forage Insect Investigations. *U. S. Dept. Agr. Leaflet* **362**.
- ARANT, F. S. 1929. Biology and control of the southern corn rootworm. *Alabama Agr. Expt. Sta. Bull.* **230**.
- ARANT, F. S. 1934. Time of turning legumes and planting corn to avoid injury from the southern corn rootworm. *Alabama Agr. Expt. Sta. Circ.* **65**.
- ARBUTHNOT, K. D. 1953. Present status and potential value of parasites of the European corn borer. *Proc. North Central States Branch Entomol. Soc. Amer.* **8**: 30-32.
- BABCOCK, K. W., and VANCE, A. M. 1929. The corn borer in central Europe, a review of investigations from 1924 to 1927. *U. S. Dept. Agr. Tech. Bull.* **135**.
- BACK, E. A. 1929. Angoumois grain moth. *U. S. Dept. Agr. Farmers' Bull.* **1156**.
- BACK, E. A., and COTTON, R. T. 1926. Biology of the saw-toothed grain beetle, *Oryzaephilus surinamensis* Linne. *J. Agr. Research* **33**: 435-452.
- BACK, E. A., and COTTON, R. T. 1926. The cadelle. *U. S. Dept. Agr. Bull.* **1428**.
- BACON, O. G., ANDERSON, L. D., and REYNOLDS, H. T. 1953. Control of corn earworm attacking sweet corn in California. *J. Econ. Entomol.* **46**: 614-620.
- BAERG, W. J. 1942. Rough-headed corn stalk-beetle. *Arkansas Agr. Expt. Sta. Bull.* **415**.
- BAKER, W. A., and BRADLEY, W. G. 1948. The European corn borer—its present status and methods of control. *U. S. Dept. Agr. Farmers' Bull.* **1548** (Rev.).
- BAKER, W. A., and QUESTEL, D. D. 1939. Investigations of insecticides for control of the European corn borer at Toledo, Ohio, 1937-1938. *J. Econ. Entomol.* **32**: 526-530.
- BAKER, W. A., BRADLEY, W. G., and CLARK, C. A. 1949. Biological control of the European corn borer in the United States. *U. S. Dept. Agr. Tech. Bull.* **983**.
- BAKER, W. A., QUESTEL, D. D., and BATCHELDER, C. H. 1942. Protecting market sweet corn from the European corn borer. *U. S. Dept. Agr. Leaflet* **225**.
- BARBER, G. W. 1925. A study of the cause of the decrease in the infestation of the European corn borer (*Pyrausta nubilalis*, Hubn.) in the New England area during 1923. *Ecology* **6**: 39-47.
- BARBER, G. W. 1936. The corn earworm in southeastern Georgia. *Georgia Agr. Expt. Sta. Bull.* **192**.

- BARBER, G. W. 1941. Hibernation of the corn earworm in southeastern Georgia. *U. S. Dept. Agr. Bull.* **791**.
- BARBER, G. W. 1942. Mineral-oil treatment of sweet corn for earworm control. *U. S. Dept. Agr. Circ.* **657**.
- BARBER, G. W. 1944. Mineral oils, alone or combined with insecticides, for control of earworms in sweet corn. *U. S. Dept. Agr. Tech. Bull.* **880**.
- BARBER, G. W., and DICKE, F. F. 1937. The effectiveness of cultivation as a control for the corn earworm. *U. S. Dept. Agr. Tech. Bull.* **561**.
- BARBER, G. W., and DICKE, F. F. 1939. Effect of temperature and moisture on overwintering pupae of the corn earworm in the northeastern states. *J. Agr. Research* **59**: 711-723.
- BATCHELDER, C. H. 1949. European corn borer location on the corn plant as related to insecticidal control. *U. S. Dept. Agr. Tech. Bull.* **976**.
- BATCHELDER, C. H., and QUESTEL, D. D. 1931. Insecticidal control of the European corn borer, the problems involved and some experimental results. *J. Econ. Entomol.* **24**: 1152-1167.
- BATCHELDER, C. H., QUESTEL, D. D., and TURNER, N. 1937. European corn borer investigations. *Connecticut Agr. Expt. Sta. Bull.* **395**.
- BENTON, C., and FLINT, W. P. 1938. The comparative attractiveness of various small grains to the chinch bug. *U. S. Dept. Agr. Circ.* **508**.
- BIGGER, J. H. 1928. Hibernation studies of *Colaspis* (Brunnea) *flavida* (Fab.) *J. Econ. Entomol.* **21**: 268-273.
- BIGGER, J. H. 1932. Short rotation fails to prevent attack of *Diabrotica longicornis* Say. *J. Econ. Entomol.* **25**: 196-199.
- BIGGER, J. H., and BAUER, F. C. 1939. Plowing dates as they affected the abundance of corn root aphids at Clayton, Illinois, 1929-1932. *J. Am. Soc. Agron.* **31**: 695-697.
- BIGGER, J. H., and PETTY, H. B. 1953. New control for chinch bugs. *Illinois Univ. Coll. Agr. Circ.* **707**.
- BIGGER, J. H., and PETTY, H. B. 1953. Reduction of corn borer numbers from October to June—a ten-year study. *Illinois Agr. Expt. Sta. Bull.* **566**.
- BIGGER, J. H., SNELLING, R. O., and BLANCHARD, R. A. 1941. Resistance of corn strains to the southern corn rootworm *Diabrotica undecimpunctata* F. *J. Econ. Entomol.* **34**: 605-613.
- BIGGER, J. H., HOLBERT, J. R., FLINT, W. P., and LANG, A. L. 1938. Resistance of certain corn hybrids to attack of southern corn rootworm. *J. Econ. Entomol.* **31**: 102-107.
- BLANCHARD, R. A. 1942. Hibernation of the corn earworm in the central and northeastern parts of the United States. *U. S. Dept. Agr. Tech. Bull.* **838**.
- BLANCHARD, R. A. 1951. Control of the fall armyworm. *Proc. North Central States Branch, Am. Assoc. Econ. Entomol.* **6**: 69-71.
- BLANCHARD, R. A., and CHAMBERLIN, T. R. 1948. Tests of insecticides, including DDT, against the corn earworm and fall armyworm in corn. *J. Econ. Entomol.* **41**: 928-935.
- BLANCHARD, R. A., and DOUGLAS, W. A. 1953. The corn earworm as an enemy of field corn in the eastern states. *U. S. Dept. Agr. Farmers' Bull.* **1651**.
- BLANCHARD, R. A., and WENE, G. P. 1953. Control of corn earworm on sweet corn in the Lower Rio Grande Valley. 1953. *Rio Valley Hort. Inst., Proc.* **7**, 122-28.
- BLANCHARD, R. A., BIGGER, J. H., and SNELLING, R. O. 1941. Resistance of corn strains to the corn earworm. *J. Am. Soc. Agron.* **33**: 344-350.
- BLATCHLEY, W. S. 1920. "Orthoptera of Northeastern America." Nature Publishing Co., Indianapolis, Indiana.

- BRANDES, E. W. 1920. Mosaic disease of corn. *J. Agr. Research* **19**: 517-525.
- BRETT, C. H. 1953a. Fall armyworm control on late planted sweet corn. *J. Econ. Entomol.* **46**: 714-715.
- BRETT, C. H. 1953b. Southern cornstalk borer control with methoxychlor, DDT, isodrin and endrin. *J. Econ. Entomol.* **46**: 176.
- BURKHARDT, C. C. 1952. Feeding and pupating of fall armyworm in corn. *J. Econ. Entomol.* **45**: 1035-1037.
- CAFFREY, D. J., and WORTHLEY, J. H. 1927. A progress report on the investigations of the European corn borer. *U. S. Dept. Agr. Bull.* **1746**.
- CARTER, W. 1941. *Peregrinus maidis* (Ashm.) and the transmission of corn mosaic. I. Incubation period and longevity of the virus in the insect. *Ann. Entomol. Soc. Amer.* **34**: 551-556.
- CARTWRIGHT, O. L. 1929. The maize billbug in South Carolina. *South Carolina Agr. Expt. Sta. Bull.* **257**.
- CARTWRIGHT, O. L. 1930. The rice weevil and associated insects in relation to shuck length and corn varieties. *South Carolina Agr. Expt. Sta. Bull.* **266**.
- CARTWRIGHT, O. L. 1934. The southern corn stalk borer in South Carolina. *South Carolina Agr. Expt. Sta. Bull.* **294**.
- CHAMBERLIN, T. R., and CALLENBACH, J. A. 1943. Oviposition of June beetles and the survival of their offspring in grasses and legumes. *J. Econ. Entomol.* **36**: 681-688.
- CHITTENDEN, F. H. 1916. The pink corn-worm. An insect destructive to corn in the crib. *U. S. Dept. Agr. Bull.* **363**.
- CHRISTENSEN, J. J., and SCHNEIDER, C. L. 1950. European corn borer (*Pyrausta nubilalis* Hbn.) in relation to shank, stalk, and ear rots of corn. *Phytopathology* **40**: 284-291.
- COLLINS, G. N., and KEMPTON, J. H. 1917. Breeding sweet corn resistant to the corn earworm. *J. Agr. Research* **11**: 549-572.
- COON, B. F., MILLER, R. C., and AURAND, L. W. 1948. Correlation between the carotene content of corn and infestation by the corn leaf aphid. *Pennsylvania Agr. Expt. Sta. J. Ser.* **1436**.
- COON, B. F. 1951. Japanese beetle damage in field corn. *Pennsylvania Agr. Expt. Sta., Progr. Rept.* **55**.
- COTTON, R. T. 1920. Rice weevil (*Calandra*) *Sitophilis oryza*. *J. Agr. Research* **20**: 409-422.
- COTTON, R. T. 1938. Control of insects attacking grain in farm storage. *U. S. Dept. Agr. Farmers' Bull.* **1811**.
- COTTON, R. T. 1947. "Insect Pests of Stored Grain and Grain Products." Burgess Publishing Co., Minneapolis, Minnesota.
- COTTON, R. T., WALKDEN, H. H., WHITE, C. D., and WILBUR, D. A. 1953. Causes of outbreaks of stored-grain insects. *North Central Regional Publ.* **35**.
- COX, H. C., and LILLY, J. H. 1953. Chemical control of the corn rootworm. *J. Econ. Entomol.* **46**: 217-224.
- CRAWFORD, H. G., and SPENCER, G. J. 1922. The European corn borer (*Pyrausta nubilalis* Hubn.): Life history in Ontario. *Ann. Rept. Entomol. Soc. Ontario* **52nd**, pp. 22-26.
- CRUMB, S. E. 1929. Tobacco cutworms. *U. S. Dept. Agr. Tech. Bull.* **88**.
- DAVIS, E. G., HORTON, J. R., GABLE, C. H., WALTER, E. V., and BLANCHARD, R. A. 1933. The southwestern corn borer. *U. S. Dept. Agr. Tech. Bull.* **388**.
- DAVIS, J. J. 1922. Common white grubs. *U. S. Dept. Agr. Farmers' Bull.* **940**.
- DAVIS, J. J. 1949. The corn root aphid and methods of controlling it. *U. S. Dept. Agr. Farmers' Bull.* **891**.

- DAVIS, J. J., and SATTERTHWAIT, A. F. 1916. Life-history studies of *Pseudaletia* (Cirphis) *unipuncta*, the true armyworm. *J. Agr. Research* **6**: 799–812.
- DEAN, G. A. 1913. Mill and stored-grain insects. *Kansas Agr. Expt. Sta. Bull.* **189**.
- DECKER, G. C. 1941. Protect Iowa's grain crop. *Iowa State Col. 42nd Yearbook* (Pt. 4), pp. 168–176.
- DECKER, G. C. 1943. Toxic-dust barriers for chinch bug control. *J. Econ. Entomol.* **36**: 658–661.
- DECKER, G. C., and BIGGER, J. H. 1949. Spraying and dusting field corn for corn borer control. *Illinois Univ. Coll. Agr. Circ.* **642**.
- DECKER, G. C., BIGGER, J. H., and WEIMAN, C. J. 1953. Spraying the margins of fields as a substitute for barrier construction in chinch bug control. *J. Econ. Entomol.* **46**: 316–320.
- DICKE, F. F. 1939. Seasonal abundance of the corn earworm. *J. Agr. Research* **59**: 237–257.
- DICKE, F. F., and JENKINS, M. T. 1945. Susceptibility of certain strains of field corn in hybrid combinations to damage by corn earworms. *U. S. Dept. Agr. Tech. Bull.* **898**.
- DICKE, F. F., and PENNY, L. H. 1952. Built-in resistance helps corn fight borers. *What's New in Crops & Soils* **4**: 9–11.
- DITMAN, L. P. 1938. Metabolism in the corn earworm. Studies on fat and water. *Maryland Agr. Expt. Sta. Bull.* **414**.
- DITMAN, L. P., and CORY, E. N. 1931. The corn earworm biology and control. *Maryland Agr. Expt. Sta. Bull.* **328**.
- DITMAN, L. P., WEILAND, G. S., and GUILL, J. H., JR. 1940. The metabolism in the corn earworm. *J. Econ. Entomol.* **33**: 282–295.
- DOUGLAS, W. A. 1948. The effect of husk extension and tightness on earworm damage to corn. *J. Econ. Entomol.* **40**: 661–664.
- DOUGLAS, W. A., and SMITH, C. E. 1953. Control of the corn earworm and rice weevil in dent corn with DDT-mineral oil emulsions. *J. Econ. Entomol.* **46**: 683–684.
- EDEN, W. G. 1952. Effects of kernel characteristics and components of husk cover on rice weevil damage to corn. *J. Econ. Entomol.* **45**: 1084–1085.
- EDEN, W. G., and ARANT, F. S. 1953. Control of corn rootworm in corn. *Alabama Agr. Expt. Sta. Leaflet* **34**.
- EICHMANN, R. D. 1940. Corn earworm hibernates in Washington State. *J. Econ. Entomol.* **33**: 951–952.
- ELLIOTT, C., and POOS, F. W. 1934. Overwintering of *Aplanobacter stewarti*. *Science* **80**: 289–290.
- ELLIOTT, C., and POOS, F. W. 1940. Seasonal development, insect vectors, and host range of bacterial wilt of sweet corn. *J. Agr. Research* **60**: 645–686.
- FLINT, W. P. 1921. Chinch bug resistance shown by certain varieties of corn. *J. Econ. Entomol.* **14**: 83–85.
- FLINT, W. P., DUNGAN, G. H., and BIGGER, J. H. 1934. Fighting the cinch bug on Illinois farms. *Illinois Agr. Expt. Sta. Circ.* **419**.
- FLOYD, E. H., and SMITH, C. E. 1949. Control of the southern corn rootworm and the seed-corn maggot in Louisiana. *J. Econ. Entomol.* **42**: 908–910.
- FLOYD, E. H., and SMITH, C. E. 1953. Pyrethrum and lindane in the protection of corn and rough rice from stored grain insects. *J. Econ. Entomol.* **46**: 771–774.
- FORBES, S. A. 1893. Noxious and beneficial insects of Illinois. *Illinois State Entomol. Rept.* **18**.

- FORBES, S. A. 1905. Noxious and beneficial insects of the State of Illinois. *Illinois State Entomol. Rept.* **23**.
- FORBES, S. A. 1915. Recent Illinois work on the corn root-aphid and the control of its injuries. *Illinois Agr. Expt. Sta. Bull.* **178**.
- FULTON, B. B. 1946. Soil insecticides for the control of the southern corn rootworm. *J. Econ. Entomol.* **39**: 781-783.
- GARMAN, H., and JEWETT, H. H. 1914. The life-history and habits of the corn-earworm (*Chloridea obsoleta*). *Kentucky Agr. Expt. Sta. Bull.* **187**.
- GILLETTE, C. P. 1912. *Diabrotica virgifera* Lec. A corn rootworm. *J. Econ. Entomol.* **5**: 364-366.
- GLEN, R., KING, K. M., and ARNASON, A. P. 1943. The identification of wireworms of economic importance in Canada. *Can. J. Research* **21**: 358-387.
- GOOD, N. E. 1936. The flour beetles of the genus *Tribolium*. *U. S. Dept. Agr. Tech. Bull.* **498**.
- GUNDERSON, H. 1953. Stored grain insects. *Iowa State Coll. Ext. Serv. Pamphlet* **205**.
- HADLEY, C. H., and HAWLEY, T. M. 1934. General information about the Japanese beetle in the United States. *U. S. Dept. Agr. Circ.* **332**.
- HAMILTON, C. C. 1935. The control of insect pests of lawns and golf courses. *New Jersey Circ.* **347**.
- HAWKINS, J. H. 1936. The bionomics and control of wireworms in Maine. *Maine Agr. Expt. Sta. Bull.* **381**.
- HAWLEY, I. M. 1922. Insects and other animal pests injurious to field beans in New York. *New York (Cornell) Agr. Expt. Sta. Mem.* **55**.
- HAWLEY, I. M., and METZGER, F. W. 1940. Feeding habits of the adult Japanese beetle. *U. S. Dept. Agr. Circ.* **547**.
- HAYSLIP, N. C., KELSHEIMER, E. G., THAMES, W. H., JR., and WILSON, J. W. 1953. Corn earworm investigations in Florida. *J. Econ. Entomol.* **46**: 574-582.
- HEADLEE, T. J., and MCCOLLOCH, J. W. 1913. The chinch bug. *Kansas Agr. Expt. Sta. Bull.* **191**.
- HILL, R. E., HIXON, E., and MUMA, M. H. 1948. Corn rootworm control tests with Benzene Hexachloride, DDT, nitrogen fertilizers and crop rotations. *J. Econ. Entomol.* **41**: 392-401.
- HINDS, W. E. 1914. Reducing insect injury in stored corn. *J. Econ. Entomol.* **7**: 203-211.
- HOLBERT, J. R., FLINT, W. P., and BIGGER, J. H. 1934. Chinch bug resistance in corn—an inherited character. *J. Econ. Entomol.* **27**: 121-124.
- HOLBERT, J. R., FLINT, W. P., BIGGER, J. H., and DUNGAN, G. H. 1935. Resistance and susceptibility of corn strains to second brood chinch bugs. *Iowa State J. Sci.* **9**: 413-425.
- HUBER, L. L., and STRINGFIELD, G. H. 1942. Aphid infestation of strains of corn as an index of their susceptibility to corn borer attack. *J. Agr. Research* **64**: 283-291.
- HUBER, L. L., NEISWANDER, C. R., and SALTER, R. M. 1928. The European corn borer and its environment. *Ohio Agr. Expt. Sta. Bull.* **429**.
- HYSLOP, J. A. 1915. Wireworms attacking cereal and forage crops. *U. S. Dept. Agr. Bull.* **156**.
- INGRAM, J. W., and BYNUM, E. K. 1941. The sugercane borer. *U. S. Dept. Agr. Farmers' Bull.* **1884**.
- INGRAM, J. W., BYNUM, E. K., MATHES, R., HALEY, W. E., and CHARPENTIER, L. J. 1951. Pests of sugarcane and their control. *U. S. Dept. Agr. Circ.* **878**.
- ISELY, D. 1929. The southern corn rootworm. *Arkansas Agr. Expt. Sta. Bull.* **232**.

- ISELY, D. 1935. Relation of hosts to abundance of cotton bollworm. *Arkansas Agr. Expt. Sta. Bull.* **320**.
- ISELY, D., and MINER, F. D. 1944. The lesser cornstalk borer, a pest of fall beans. *J. Kansas Entomol. Soc.* **17**: 51-57.
- JEWETT, H. H. 1942. Life history of the wireworm *Aeolus mellillus* (Say). *Kentucky Agr. Expt. Sta. Bull.* **425**.
- KELLY, E. O. G. 1911. Papers on cereal and forage insects. The maize billbug. *U. S. Dept. Agr. Bur. Entomol. Bull.* **95** (Pt. II).
- KELSHEIMER, E. G., HAYSLIP, N. C., and WILSON, J. W. 1950. Control of budworms, earworms and other insects attacking sweet corn and green corn in Florida. *Florida Agr. Expt. Sta. Bull.* **466**.
- KNECHTEL, W. K., and MANOLACHE, C. 1944. Neue Blattläuse für Rumänien. *Bull. Sect. sci. acad. roumaine* **26**: 690-702.
- KNIGHT, H. H. 1916. The armyworm in New York in 1914. *Cornell Univ. Agr. Expt. Sta. N. Y. State Coll. Agr. Bull.* **376**.
- KOEHLER, B. 1942. Natural mode of entrance of fungi into corn ears and some symptoms that indicate infection. *J. Agr. Research* **64**: 421-442.
- KUITERT, L. C., and CONNIN, R. V. 1952. Biology of the American grasshopper in the southeastern states. *Florida Entomologist* **31**: 22-33.
- KUITERT, L. C., and CONNIN, R. V. 1953. Grasshoppers and their control. *Florida Agr. Expt. Sta. Bull.* **516**.
- KUNKEL, L. O. 1921. A possible causative agent for the mosaic disease of corn. *Hawaiian Sugar Planters' Assoc. Expt. Sta. Bull.* **3**: 44-58.
- KUNKEL, L. O. 1946. Leafhopper transmission of corn stunt. *Proc. Natl. Acad. Sci.* **32**: 246-247.
- KUNKEL, L. O. 1948. Studies on a new corn virus disease. *Arch. ges. Virusforsch.* **4**: 24-46.
- KYLE, C. H. 1918. Shuck protection for ear corn. *U. S. Dept. Agr. Bull.* **708**.
- LANE, M. C. 1941. Wireworms and their control on irrigated lands. *U. S. Dept. Agr. Farmers' Bull.* **1866**.
- LEIBY, R. W. 1920. The larger corn stalk-borer in North Carolina. *North Carolina Dept. Agr.* **411**, Whole No. **274**.
- LILLY, J. H., and GUNDERSON, H. 1953. Insecticides for soil insects. *Iowa Farm Sci.* **7**: 15-17.
- LINDSAY, D. R. 1943. The biology and morphology of *Colaspis flavida* (Say). *Iowa State Coll. J. Sci.* **18**: 60-61.
- LUGINBILL, P. 1918. The southern corn rootworm and farm practices to control it. *U. S. Dept. Agr. Farmers' Bull.* **950**.
- LUGINBILL, P. 1922. Bionomics of the chinch bug. *U. S. Dept. Agr. Bull.* **1016**.
- LUGINBILL, P. 1928. The fall armyworm. *U. S. Dept. Agr. Tech. Bull.* **34**.
- LUGINBILL, P. 1950. Habits and controls of the fall armyworm. *U. S. Dept. Agr. Farmers' Bull.* **1990**.
- LUGINBILL, P., and AINSLIE, G. G. 1917. The lesser corn stalk-borer. *U. S. Dept. Agr. Bull.* **539**.
- LUGINBILL, P., SR., and CHAMBERLIN, T. R. 1953. Control of common white grubs in cereal and forage crops. *U. S. Dept. Agr. Farmers' Bull.* **1798**.
- LUGINBILL, P., SR., and PAINTER, H. R. 1953. May beetles of the United States and Canada. *U. S. Dept. Agr. Tech. Bull.* **1060**.
- MARSTON, A. R. 1931. Breeding European corn borer resistant corn. *J. Am. Soc. Agron.* **23**: 960-964.

- McCOLLOCH, J. W. 1921. The corn leaf aphid, *Aphis maidis* Fitch, in Kansas. *J. Econ. Entomol.* **14**: 89-94.
- METCALF, C. L., FLINT, W. P., and METCALF, R. L. 1951. "Destructive and Useful Insects Their Habits and Control," 3rd ed. McGraw-Hill Book Company, Inc., New York.
- METCALF, Z. P. 1917. Biological investigation of *Sphenophorus callosus* Oliv. *North Carolina Agr. Expt. Sta. Tech. Bull.* **13**.
- MEYERS, M. T., HUBER, L. L., NEISWANDER, C. R., RICHEY, F. D., and STRINGFIELD, G. H. 1937. Experiments on breeding corn resistant to the European corn borer. *U. S. Dept. Agr. Tech. Bull.* **583**.
- NEISWANDER, C. R. 1926. The sources of American corn insects, 98 pp. Ph.D. dissertation, Ohio State University, Columbus.
- NIEDERHAUSER, J. S., and CERVANTES, J. 1950. Transmission of corn stunt in Mexico by a new vector, *Baldulus elimatus*. Abstract *Phytopathology* **40**: 20-21.
- NOBLE, W. B. 1932. Sod webworms and their control in lawns and golf greens. *U. S. Dept. Agr. Circ.* **248**.
- PACKARD, C. M. 1946. DDT dusts and sprays, and bran baits containing different poisons for armyworm control. *J. Econ. Entomol.* **39**: 669.
- PACKARD, C. M., LUGINBILL, P., SR., and BENTON, C. 1950. How to fight the chinch bug. *U. S. Dept. Agr. Farmers' Bull.* **1780**.
- PAINTER, R. H. 1928. Notes on the injury to plant cells by chinch bug feeding. *Ann. Entomol. Soc. Amer.* **21**: 232-242.
- PAINTER, R. H., and BRUNSON, A. M. 1940. Differential injury within varieties, inbred lines, and hybrids of field corn caused by the corn earworm *Heliothis armigera* (Hbn.). *J. Agr. Research* **61**: 81-100.
- PAINTER, R. H., SNELLING, R. O., and BRUNSON, A. M. 1935. Hybrid vigor and other factors in relation to chinch bug resistance in corn. *J. Econ. Entomol.* **28**: 1025-1030.
- PARKER, J. R. 1930. Some effects of temperature and moisture upon *Melanoplus mexicanus* Saussure and *Camnula pellucida* Scudder. *Montana Agr. Expt. Sta. Bull.* **223**.
- PARKER, J. R. 1954. Grasshoppers new look at an ancient enemy. *U. S. Dept. Agr. Farmers' Bull.* **2064**.
- PATCH, L. H. 1937. Resistance of a single-cross hybrid strain of field corn to European corn borer. *J. Econ. Entomol.* **30**: 271-278.
- PATCH, L. H. 1943. Survival, weight, and location of European corn borers feeding on resistant and susceptible field corn. *J. Agr. Research* **66**: 7-19.
- PATCH, L. H., and EVERLY, R. T. 1945. Resistance of dent corn inbred lines to survival of first-generation European corn borer larvae. *U. S. Dept. Agr. Tech. Bull.* **893**.
- PATCH, L. H., HOLBERT, J. R., and EVERLY, R. T. 1942. Strains of field corn resistant to the survival of the European corn borer. *U. S. Dept. Agr. Tech. Bull.* **823**.
- PATCH, L. H., STILL, G. W., APP, B. A., and CROOKS, C. A. 1941. Comparative injury by the European corn borer to open-pollinated and hybrid field corn. *J. Agr. Research* **63**: 355-368.
- PATCH, L. H., STILL, G. W., SCHLOSBERG, M., and BOTTGGER, G. T. 1942. Factors determining the reduction in yield of field corn by the European corn borer. *J. Agr. Research* **65**: 473-482.
- PEPPER, B. P., and CARRUTH, L. A. 1945. A new plant insecticide for control of the European corn borer. *J. Econ. Entomol.* **38**: 59-66.

- PEPPER, B. P., and HAENSELER, C. M. 1944. Control of the European corn borer and ear smut on sweet corn with dusts and sprays. *New Jersey Agr. Expt. Sta. Circ.* **486**.
- PHILLIPS, W. J. 1909. The slender seed-corn ground beetle. *U. S. Dept. Agr. Bur. Entomol. Bull.* **85** (Pt. II).
- PHILLIPS, W. J., and BARBER, G. W. 1929. A study of hibernation of the corn earworm in Virginia. *Virginia Agr. Expt. Sta. Tech. Bull.* **40**.
- PHILLIPS, W. J., and BARBER, G. W. 1931. The value of husk protection to corn ears in limiting corn earworm injury. *Virginia Agr. Expt. Sta. Tech. Bull.* **43**.
- PHILLIPS, W. J., and BARBER, G. W. 1933. Egg-laying habits and fate of eggs of the corn earworm moth and factors affecting them. *Virginia Agr. Expt. Sta. Tech. Bull.* **47**.
- PHILLIPS, W. J., and BARBER, G. W. 1934. Ear-worm injury in relation to date of planting field corn in central Virginia. *Virginia Agr. Expt. Sta. Tech. Bull.* **55**.
- PHILLIPS, W. J., and FOX, H. 1924. The rough-headed corn stalk-beetle. *U. S. Dept. Agr. Dept. Bull.* **1267**.
- PHILLIPS, W. J., UNDERHILL, C. W., and POOS, F. W. 1921. The larger corn stalk-borer in Virginia. *Virginia Agr. Expt. Sta. Tech. Bull.* **22**.
- POOS, F. W. 1938. Insects in relation to diseases of cereal and forage crops. *J. Econ. Entomol.* **31**: 24-38.
- POOS, F. W. 1945. DDT to control corn flea beetle on sweet corn and potato leafhopper on alfalfa and peanuts. *J. Econ. Entomol.* **38**: 197-199.
- POOS, F. W., and ELLIOT, C. 1936. Certain insect vectors of *Aplanobacter stewarti*. *J. Agr. Research* **52**: 585-608.
- QUAINTANCE, A. L., and BRUES, C. T. 1905. The cotton bollworm. *U. S. Dept. Agr. Bull.* **50**.
- RAND, F. V., and CASH, L. C. 1933. Bacterial wilt of corn. *U. S. Dept. Agr. Tech. Bull.* **362**.
- RAUN, E. S. 1953. Control of grasshoppers, cutworms, and armyworms in Iowa. *Proc. North Central States Branch Entomol. Soc. Amer.* **8**: 41-42.
- REDLINGER, L. M., WILSON, B. R., COTTON, R. T., and WALKDEN, H. H. 1953. Evaluation of fumigants for shelled corn. *U. S. Dept. Agr. Bur. Entomol. Plant Quarantine* **E-855**.
- REID, W. J., JR. 1940. Biology of the seed-corn maggot in the coastal plain of the south Atlantic states. *U. S. Dept. Agr. Tech. Bull.* **723**.
- SATTERTHWAIT, A. F. 1932. How to control billbugs destructive to cereal and forage crops. *U. S. Dept. Agr. Farmers' Bull.* **1003** (Rev.).
- SCHLOSBERG, M., and BAKER, W. A. 1948. Tests of sweet corn lines for resistance to European corn borer larvae. *J. Agr. Research* **77**: 137-156.
- SHELFORD, V. E., and FLINT, W. P. 1943. Populations of the chinch bug in the upper Mississippi Valley from 1823-1940. *Ecology* **24**: 435-455.
- SHOTWELL, R. L. 1939. The species and distribution of grasshoppers in the 1938 outbreak. *U. S. Dept. Agr. Bur. Entomol. Plant Quarantine Insect Pest Survey. Bull.* **19** (Suppl. 4); 179-269.
- SHOTWELL, R. L. 1941. Life history and habits of some grasshoppers of economic importance on the Great Plains. *U. S. Dept. Agr. Tech. Bull.* **774**.
- SHOTWELL, R. L. 1942. Evaluation of baits and bait ingredients used in grasshopper control. *U. S. Dept. Agr. Tech. Bull.* **793**.
- SHOTWELL, R. L. 1949. The comparative effectiveness of poisoned bait and sprays for grasshopper control in Lyman County, South Dakota, 1947. *U. S. Dept. Agr. Bur. Entomol. Plant Quarantine* **E-771**.

- SHOTWELL, R. L. 1952. Tests with sprays for controlling grasshoppers on farm lands in North Dakota and Texas, 1950-51. *U. S. Dept. Agr. Bur. Entomol. Plant Quarantine* **E-845**.
- SHOTWELL, R. L. 1954. Status of the European corn borer in 1953. *U. S. Plant Pest Control Branch, Econ. Ins't. Rept.* **4**: 105-126.
- SIMANTON, F. L., DICKE, F. F., and BOTTGER, G. T. 1931. The lethal power of certain insecticides tested in Michigan against the European corn borer. *J. Econ. Entomol.* **24**: 395-404.
- SIMMONS, P., and ELLINGTON, G. W. 1933. Life history of the Angoumois grain moth of Maryland. *U. S. Dept. Agr. Tech. Bull.* **351**.
- SNELLING, R. O., BLANCHARD, R. A., and BIGGER, J. H. 1940. Resistance of corn strains to the leaf aphid *Aphis maidis* Fitch. *J. A. Soc. Agron.* **32**: 371-381.
- STANLEY, W. W. 1936. Studies of the ecology and control of cutworms in Tennessee. *Tennessee Agr. Expt. Sta. Bull.* **159**.
- STIRRETT, G. M. 1938. A field study of the flight, oviposition, and establishment periods of the cycle of the European corn borer, *Pyrausta nubilalis* Hbn., and the physical factors affecting them. *Sci. Agr.* **18**: 355-369, 536-557, 568-585, 656-683.
- STONER, W. U. 1952. Leaf fleck, an aphid borne virus disease of maize. *Phytopathology* **42**: 683-689.
- STOREY, H. H. 1925. The transmission of streak disease of maize by the leafhopper, *Cicadulina (Balclutha) mbila* Naude. *Ann. Appl. Biol.* **12**: 422-439.
- STOREY, H. H. 1937. A new virus of maize transmitted by *Cicadulina* spp. *Ann. Appl. Biol.* **24**: 87-94.
- STOREY, H. H. 1939. Transmission of plant viruses by insects. *Botan. Rev.* **5**: 240-272.
- TATE, H. D., and BARE, O. S. 1946. Corn rootworms. *Nebraska Agr. Expt. Sta. Bull.* **381**.
- TENHET, J. N., and HOWE, E. W. 1939. The sand wireworm and its control in South Carolina coastal plain. *U. S. Dept. Agr. Tech. Bull.* **659**.
- THOMAS, C. A. 1940. The biology and control of wireworms. *Pennsylvania Agr. Expt. Sta. Bull.* **392**.
- VICKERY, R. A. 1929. Studies on the fall armyworm in the gulf coast district of Texas. *U. S. Dept. Agr. Tech. Bull.* **138**.
- VINAL, S. C. 1917. The European corn borer *Pyrausta nubilalis* Hubner, a recently established pest in Massachusetts. *Massachusetts Agr. Expt. Sta. Bull.* **178**.
- VINAL, S. C., and CAFFREY, D. J. 1919. The European corn borer and its control. *Massachusetts Agr. Expt. Sta. Bull.* **189**.
- WALKDEN, H. H. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. *U. S. Dept. Agr. Circ.* **849**.
- WALKDEN, H. H., and SCHWITZGEBEL, R. B. 1951. Evaluation of fumigants for control of insects attacking wheat and corn in steel bins. *U. S. Dept. Agr. Bull.* **1045**.
- WALTER, E. V. 1951. The development of sweet corn varieties resistant to the corn earworm. *Proc. North Central States Branch Entomol. Soc. Amer.* **6**: 13-14.
- WALTER, E. V., and BRUNSON, A. M. 1940. Differential susceptibility of corn hybrids to *Aphis maidis*. *J. Econ. Entomol.* **33**: 623-628.
- WALTER, E. V., and BRUNSON, A. M. 1946. Selection for aphid resistance within inbred lines of maize. *J. Am. Soc. Agron.* **38**: 974-977.
- WALTON, R. R., and BIEBERDORF, G. A. 1948. Seasonal history of the southwestern corn borer *Diatraea grandiosella* Dyar, in Oklahoma; and experiments on methods of control. *Oklahoma Agr. Expt. Sta. Tech. Bull.* **7-32**.

- WALTON, W. R., and PACKARD, C. M. 1951. The armyworm and its control. *U. S. Dept. Agr. Farmers' Bull.* **1850**.
- WEBSTER, F. M. 1913a. The southern corn rootworm or budworm. *U. S. Dept. Agr. Bull.* **5**.
- WEBSTER, F. M. 1913b. The western corn rootworm. *U. S. Dept. Agr. Bur. Entomol. Bull.* **8**.
- WELLMAN, F. L. 1934. Infection of *Zea mays* and various other gramineae by the celery virus in Florida. *Phytopathology* **24**: 1035-1037.
- WENE, G. P., BLANCHARD, R. A., and WALTER, E. V. 1952. Relation of corn earworm resistance in sweet corn to efficiency of insecticide sprays. *J. Econ. Entomol.* **45**: 931-933.
- WILBUR, D. A., BRYSON, H. R., and PAINTER, R. H. 1950. Southwestern corn borer in Kansas. *Kansas Agr. Expt. Sta. Bull.* **339**.
- WILDERMUTH, V. L. 1917. The desert corn flea-beetle. *U. S. Dept. Agr. Bull.* **436**.
- WILDERMUTH, V. L., and WALTER, E. V. 1932. Biology and control of the corn leaf aphid with special reference to the southwestern states. *U. S. Dept. Agr. Tech. Bull.* **306**.

CHAPTER XIV

Industrial Utilization

G. F. SPRAGUE

I. Introduction

The percentage of the annual U.S. corn crop which is used in industry is rather small, averaging approximately 9 per cent. This percentage represents an average yearly consumption of about 250,000,000 bu. Consumption as expressed in either of these terms fails to provide any real indication of the important and varied role corn products play in the economy of the United States.

For purposes of convenience industrial utilization may be divided into three categories: wet milling, dry milling, and fermentation. This classification is not mutually exclusive, since an organization may produce both milled and fermentation products. If fermentation is a separate enterprise, a part of the carbohydrate material may have its origin in either the wet- or dry-milling industry.

Carbohydrate sources other than corn are also used in industrial fermentation, but these will not be covered in this report.

The distribution and utilization of the corn crop in terms of total disappearance is illustrated in Table I. It will be noted that wet milling accounts for the largest portion of the corn used in industry, followed in order by dry milling and fermentation. These three industrial outlets will be discussed in order of their percentage utilization of the corn crop.

The purpose of this chapter is to present a general picture of corn milling and the industrial uses of corn. No attempt will be made to describe the various processes in detail or to present a complete account of the chemical aspects of either the wet-milling or fermentation industries. The literature on these two subjects is voluminous, and only selected general references are listed in the literature citations.

II. Wet Milling

In wet process milling the grain is first steeped, and then by progressive grinding and manipulation the germ and hull are separated from the ground endosperm. Additional manipulations permit a separation of the ground endosperm into its principal components, cell wall

or fiber, starch, protein or gluten, and solubles. Each of these separated products is further modified or refined before it reaches the ultimate consumer.

These various separations and modifications require a high degree of chemical control during the entire process to ensure the necessary degree of uniformity in the final product. This need for control has led, possibly indirectly, to intensive research on the chemical properties of

TABLE I
UTILIZATION OF U.S. CORN CROP FOR THE YEARS 1942-1951^a
(In thousands of bushels)

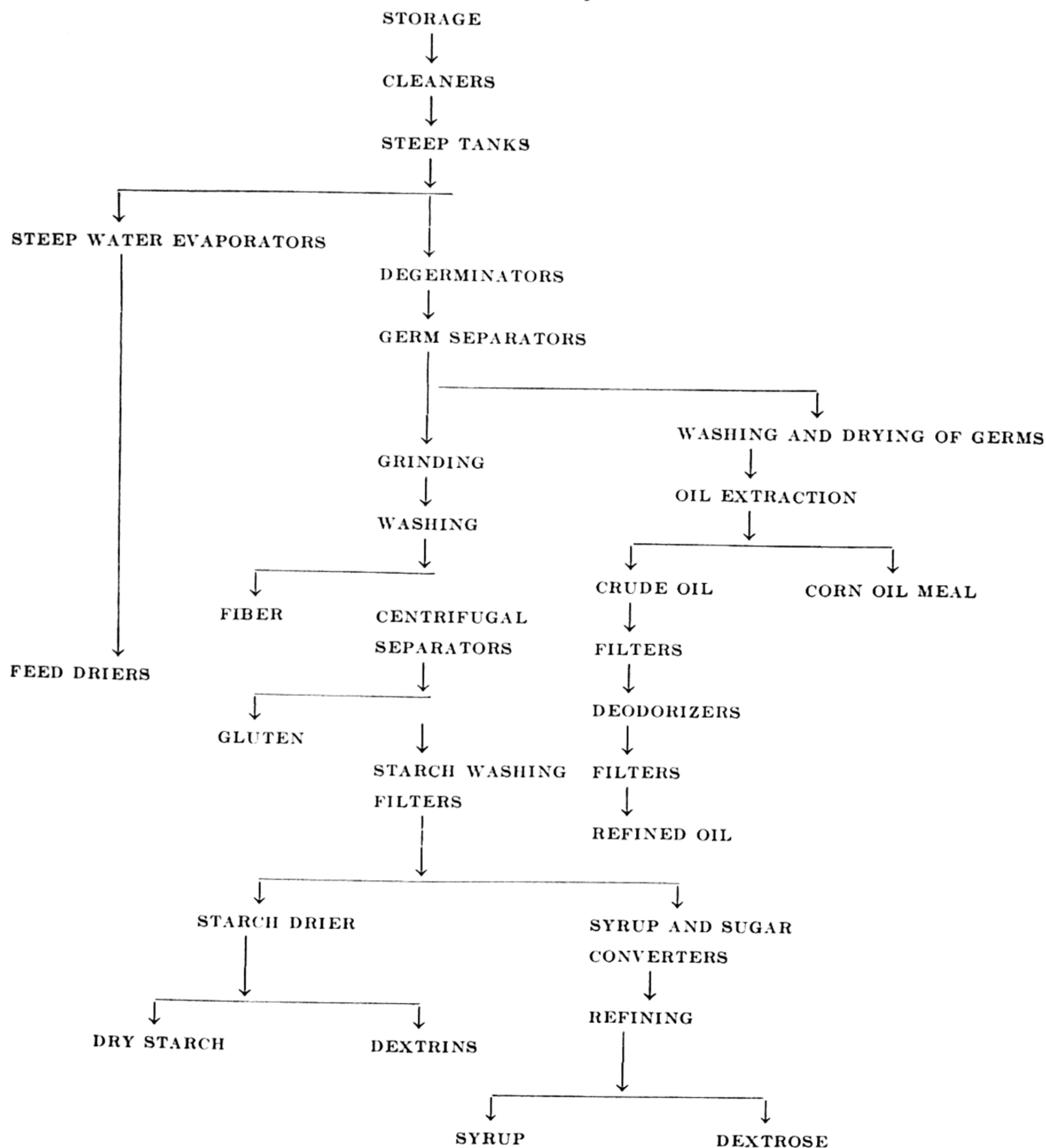
Year beginning October	Dry-processing products			Alcohol and		Seed	Livestock feed	Exports	Total disap- pearance
	Break- fast foods	Farm house- hold use	Corn- meal grits, etc.	Wet- process products	dis- tilled spirits				
1942	11,000	21,583	67,000	128,002	41,584	13,140	2,909,390	4,805	3,196,504
1943	12,000	21,053	69,000	120,934	10,482	13,298	2,866,010	9,997	3,122,774
1944	12,000	19,487	70,000	124,589	36,986	12,433	2,717,664	16,611	3,009,770
1945	11,000	18,589	64,000	111,732	27,513	12,382	2,747,752	19,874	3,012,842
1946	10,600	17,031	70,000	143,457	55,294	11,845	2,671,271	126,740	3,106,238
1947	10,500	16,582	65,000	110,217	30,426	11,912	2,263,756	6,789	2,515,182
1948	10,000	16,219	66,000	117,009	30,260	11,618	2,554,086	111,071	2,916,263
1949	10,000	15,268	65,000	127,668	36,111	11,097	2,835,703	106,532	3,207,379
1950	11,000	15,156	70,000	133,191	45,191	11,154	2,771,354	107,231	3,164,277
1951	11,000	14,225	70,000	123,734	27,371	11,070	2,820,016	75,504	3,152,920

^a Taken from Table 48 Agricultural Statistics, U.S. Dept. of Agr. 1953.

starch and other carbohydrates. The final result has been an almost bewildering array of special uses for corn starch, oil, and protein.

The various phases of the wet-milling process have been described in some detail by F. W. Bartling (1940a, b, 1941a, b, c, 1942, 1943, 1944), and his descriptions have been used extensively in the preparation of this outline.

After the corn is received at the plant and cleaned, the first step in the wet-milling process is steeping. This consists of soaking corn in large tanks or vats of about 2000 to 2500 bu. capacity in warm dilute sulfurous acid solution for a period of time before grinding. The time the corn is held in the steep ranges from about 40 to 60 hours, depending upon endosperm texture, age, and moisture percentage. The sulfurous acid concentration may vary from mill to mill but is normally about 0.2 per cent. The temperatures used also vary somewhat, but 40°C. would represent a fair average. Bartling (1940a) lists the main functions of

Simplified Wet-Milling Flow Chart

steeping as: (1) to soften the corn kernel, (2) to control or inhibit the activity of microorganisms, and (3) to bleach the starch. Of these, the softening action appears to be of major importance. In addition to these purposes, there is a general feeling in the industry that the sulfurous acid brings about some dispersion of the protein, thus facilitating the separation and isolation of the starch granules. The effect of a sulfurous acid steep under laboratory conditions has been studied in some detail by Cox *et al.* (1944). Their results indicate that during steeping the protein undergoes a considerable degree of peptization which is accompanied by a disintegration and dispersion of the protein matrix in which

the starch grains are imbedded. This action cannot be satisfactorily duplicated by lactic, acetic, or hydrochloric acids at either the same percentage concentration or pH. Protein dispersion increases with the temperature of steeping over the range from 38° to 55°C. and with sulfur dioxide content from 0.0 to 0.4 per cent.

Sulfurous acid in the concentrations normally used does not completely inhibit the growth of microorganisms. Some lactic acid regularly forms during the process of steeping. Studies of steeping involving lactic acid alone or in combination with sulfurous acid suggested that lactic acid was rather ineffective in protein disintegration but was possibly somewhat more effective than sulfur dioxide in softening the corn kernel. The sulfurous acid used in steeping is commonly produced by burning sulfur to produce SO_2 , which is then absorbed in a water tower to produce acid of any desired concentration.

After steeping the softened corn is passed through a Foos mill or degerminator. Each degerminating unit consists of two large acid-resistant plates, one of which is stationary and the other rotary. The opposing surface of each plate is studded with knoblike projections. The corn, passing between these plates, is partially macerated to remove the pericarp, free the germ from the endosperm, and partially disintegrate the endosperm. This slurry of partially ground corn is then passed through a germ separator. The germ separators are long open U-shaped tanks equipped with a screw conveyor in the bottom of the tank and rotating paddles attached to the top of the tank. Before the slurry enters the tank the specific gravity is adjusted, by either the addition of water or starch washings, to facilitate the separation of the germs by flotation. The coarsely ground endosperm and the free starch particles settle to the bottom of the tank and are moved to the outlet end of the separator by the screw conveyor. The germs are moved along to an overflow outlet by the action of the rotating paddles. The germ material from the overflow outlet passes to a series of reels or shakers. The first reels are perforated metal which permit the water and starch to drain off. Some rather finely ground germs remain in the starch slurry. This material is separated by using fine screens or silk cloth. The two streams of germs may be combined and subjected to repeated washings during the screening process to remove as much starch as possible. From the final series of screens the germs are put through special squeezers or dewatering machines to reduce the moisture content, after which they are dried in steam-heated drums to further reduce the moisture content and to toughen the germ before it goes to the oil expellers.

The slurry discharged from the bottom of the first degerminators often contains germs or germ residue which has not been completely

freed from the endosperm. This requires additional grinding followed by further separation of the germs by flotation and screening. The slurry when essentially freed from germ residue still contains the hulls and endosperm fragments suspended in the starch-gluten slurry. This slurry is fed through stone buhr mills to complete the grinding of the endosperm and reduce all material to the consistency of a fine slop. This ground material is fed into a series of pitched reels moving countercurrent to a stream of water similar to that used for washing germs. Starch and gluten in suspension drain away through the perforation of the reels. The material passing through the reels consists largely of hulls and other fibrous materials. This coarse material may then be pressed to remove water or may be fed into the gluten stream at a later stage before pressing.

After the removal of the hulls and other fiber the material remaining in the liquor is starch, gluten, and various water-soluble materials. In earlier years the starch-gluten separation was made on a series of tables approximately 100 to 120 feet long and 2 feet wide with a pitch of about 6 inches. The liquor was delivered at a uniform rate of flow at the upper end of each table. The starch, having the higher specific gravity, is deposited on the table and the gluten, still in suspension, passed off the lower end of the table. After the starch on the tables has built up to capacity, the flow of liquid is shut off and the starch washed off the tables. This method of separation is still used to some extent but has been largely replaced by vacuum filters or by continuous-flow centrifugal separators. Either of these separators require much less floor space and is more efficient in delivering both starch and gluten with a high degree of purity. Regardless of how the separation has been effected, the starch must be subjected to repeated screenings and washings to remove foreign material, gluten, and solubles and to achieve the desired degree of whiteness. The washed and filtered starch may be dried or converted without drying to syrup or sugar. Drying may be achieved in a variety of differing ways ranging from tunnel kilns to flash driers. The dried starch then serves as source material for the production of edible and laundry starches, various types of modified starches, and dextrans. These will be mentioned in more detail later.

The liquor remaining after the initial starch separation contains a considerable quantity of suspended gluten and various organic and mineral substances in solution. This mixture is piped to large tanks where the gluten is allowed to settle out. The steep water may be evaporated and added to feeds or concentrated and used in culture media for the production of antibiotics.

The preceding description has presented a brief outline of the vari-

ous processes involved in the separation of the corn kernel into starch, oil, gluten, hull, and fine fiber. This separation is only a part of the wet-milling process. Each of these compounds may be considered as raw material for further refining or modification before it reaches the ultimate consumer.

The quantity of corn used by the wet-milling industry and the amounts of specified products produced are presented in Table II.

TABLE II
THE QUANTITY OF CORN PROCESSED AND THE AMOUNTS BY SPECIFIED PRODUCTS PRODUCED BY THE WET-MILLING INDUSTRY FOR THE PERIOD 1943-1952^a

Year	Products sold								
	Wet- process grindings, 1000 bu.	Corn starch, 1000 lb.	Corn sugar, 1000 lb.	Corn sirup unmixed, 1000 lb.	Dex- trines, 1000 lb.	Corn oil, 1000 lb.		Feed, 1000 tons	
						Crude	Refined	Gluten feed and meal	Corn- oil meal
1943	128,455	1,530,649	722,420	1,799,809	188,435	56,659	165,064	914	63
1944	119,928	1,240,483	684,803	1,816,326	169,790	40,134	146,526	827	55
1945	119,053	1,237,602	665,459	1,837,902	148,975	29,183	144,543	824	54
1946	120,611	1,282,726	647,902	1,837,280	140,630	30,561	136,778	872	59
1947	139,273	1,509,289	785,293	1,983,006	162,429	40,630	181,226	1015	63
1948	109,878	1,388,719	711,764	1,333,378	157,598	27,281	151,218	781	59
1949	116,174	1,499,193	737,652	1,418,215	158,591	36,213	172,698	817	51
1950	131,439	1,790,527	828,978	1,532,759	206,821	53,311	181,645	897	54
1951	129,049	1,659,000	767,269	1,549,018	188,463	49,540	171,691	961	54
1952	126,128	1,656,615	748,316	1,497,004	169,367	47,946	167,826	872	58

^a Taken from Table 49 Agricultural Statistics, U.S. Dept. Agr. 1953.

1. Starch

The glucose residues making up the starch molecule may be combined in different ways to produce different types of starches. Amylose is built up by the addition of successive glucose units to form a long relatively unbranched chain. Amylopectin, the other molecular structure found in normal corn starch, has a highly branched chain structure. Maquenne and Roux (1905) were one of the first to apply the terms “amylose” and “amylopectin” to the two types of molecules occurring in the starch granule. However, since this publication, these terms have been used to designate a wide variety of starch fractions (Kerr, 1944). The current usage had its inception with the work of K. F. Meyer and his co-workers (1940a, b, c) and many others.

Starch from most corns contains on the average about 72 per cent

of the branched and 28 per cent of the straight-chain configurations. Waxy corn starch, on the other hand, is made up exclusively of the branched-chain component. The molecular structure of starch has a pronounced effect on pasting characteristics. We shall consider first the industrial modifications and uses of normal corn starch.

/ The washed and purified starch may be processed in a number of ways to fill special industrial needs. Some of the starch is used directly, without drying, in the production of syrup and dextrose sugar. Some may be dried and used commercially in an unmodified form. Still other industrial outlets require that the starch be modified by various treatments to impart special properties to its pastes. The literature on the chemistry of starch and on its industrial utilization is tremendous, and we shall attempt to present only a very brief outline which may be informative to the general reader. For our purpose a simplified classification of starch and its by products will be used. This is as follows:

1. Thick boiling starch.
2. Thin boiling starch.
3. Dextrin and British gums.
4. Hydrolytic products (corn syrup and dextrose).

a. Thick Boiling Starches. Thick boiling starches as the name implies yield viscous solutions which set to more or less stiff jellies. They may be produced from either raw or modified starches. The various modifying agents would include heat, acid, alkali, enzymes, etc. However, these treatments are quite mild so as not to interfere with the thick boiling properties of the final paste. These modifications may be made either before or after the starch is dried.

The wet starch is usually dried in a vacuum or kiln drier. The dried product is quite variable for particle size and is screened. The starch is classified according to its physical properties as lump, pearl, or powdered. Lump and pearl starches differ primarily in the size of the granules. Powdered starch differs from the above type in particle size and if it is to be used for food purposes will also differ in purity. The lump and pearl starches are used in the production of laundry starches, as a sizing in the weaving of cotton, as a constituent of printing pastes for the dyeing of fabrics, certain types of adhesives, etc.

Powdered starch is ground to pass a 200-mesh screen and is used primarily in the food field—as a filler in baking powder, in prepared puddings, etc. The addition of small amounts of oil produces a special type known as molding starch. This is used in confectioneries in the casting of cream-center candies, etc.

/ *b. Thin Boiling Starch.* The term “thin boiling starch” is used to represent a group of modified starches having a lower viscosity than that

characteristic of normal or unmodified starch. The usual method of manufacture involves treatment with a dilute acid at temperatures slightly below that of incipient gelatinization or some form of oxidation. The acid treatment may bring about a partial hydrolysis as well as partial destruction of the granule structure. The extent of the hydrolysis appears to vary with the fluidity of the pastes; those exhibiting the greatest fluidity tend to exhibit the larger reducing values. The desired degree of modification may be controlled by variation in the degree of acidity, time of exposure, and temperature.

The thin boiling starches are used extensively in the textile industry as sizing for yarns preparatory to weaving and for "finishing" the cloth after weaving. They are also used in the production of certain types of confections such as jelly beans, gum drops, or gum slices.

Thin boiling starches with somewhat different properties may also be prepared by the oxidation of starch. This oxidation may be done in either an acid or alkaline media. Nitric acid, ammonium nitrate, chromic acid, permanganates, hydrogen peroxide, and the halogens have all been reported to produce oxidized starch (Radley, 1943). In alkaline media the use of hypohalites, permanganate, and peroxides is also reported to produce oxidation of starch. Newton and Peckham (1944) state that oxidized starch is characterized by a shorter cooking time, greater fluidity, increased adhesiveness, lower rate of congealing, and a clearer suspension than the parent starch. These properties make such starches well suited to the sizing of paper and sizing and finishing of textiles.

c. Dextrins and British Gums. The various products listed under this heading are quite variable both in their properties and in the method of preparation. In fact the products may have little more in common than that they all involve some degree of degradation of the parent material, starch.

British gums are the simplest of these products if judged by the manufacturing procedures involved. Dried and bolted starch is heated in a closed vessel with suitable agitation. The quality of the resulting product depends upon the moisture content of the starch, the temperature used and the duration of the treatment, and the subsequent cooling and aging. The resulting products at one extreme may resemble the thin boiling starches and at the other extreme appear to have undergone a considerable degree of caramelization. Each of these extremes has undergone some degree of degradation of the starch molecule with an accompanying increase in solubility and reducing substances. In many cases, however, the increase in reducing substances is not sufficiently great to account for the changed properties. The current theory assumes that

during the heating process cross linkages develop between the starch molecules. The net result of this change is to produce a starch having less of the properties associated with amylose and more of the properties associated with amylopectin.

Dextrins, as opposed to British gums, usually involve the use of some one or more agents such as acids, alkalis, enzymes, and heat to bring about the desired degree of starch degradation. Hydrochloric acid is most commonly used in the production of the acid-modified dextrins. However, other acids such as lactic, phosphoric, and sulfuric acids may be used. The starch is first acidified and then heated. Basic substances such as sodium carbonate, urea, and hypochlorite may also be used in a similar manner. Enzymatic conversion involves a somewhat different technique. This conversion would commonly be done at the plant where the starch paste is to be used rather than at the mill where the starch is isolated and refined. The starch is prepared in a slurry and gelatinized by heat and then subjected to the action of α and β amylase. Or the enzyme may be added to the slurry followed by an increase in temperature sufficient to cause gelatinization and final killing of the enzyme.

Dextrins are used in the production of many types of adhesives ranging from the remoistening glues characteristic of envelope flaps to molding adhesives. It is often necessary to use additional substances such as urea and borax to impart the special adhesive characteristics necessary for a particular industrial requirement.

d. Waxy Starch. Genetic variants, identified by the production of red staining starch when treated with iodine, are known in several of the cereals. Chemical studies indicate that such red staining starches are characterized by a branched-chain structure. Associated with this branched structure are certain important modifications of their unmodified starch pastes. The hot viscosities of the starch pastes are comparable to those characteristic of the tuber starches, of which tapioca is the most important (Hixon and Sprague, 1942). This fundamental difference in starch properties has been known for some time, but little attempt was made to use these peculiar cereal starches commercially until World War II. At that time tapioca imports, largely from the Dutch East Indies, were cut off. Since starches having the characteristic of those produced from tapioca were felt to be indispensable, the commercial production of waxy corn and sorghum starches was undertaken. The production and utilization of waxy sorghum starch has been rather erratic, and our presentation here will be confined to waxy corn.

Waxy corn was found in China and was first reported by Collins in 1909. Beginning in 1936 considerable work has been done by the

United States Department of Agriculture and the Iowa Agriculture Experiment Station to develop waxy hybrids having satisfactory agronomic characteristics. Hybrids were available and limited commercial production was undertaken in 1943. The acreage devoted to waxy corn has increased rather steadily since that date. The production and milling of waxy corn are essentially similar to those for ordinary corn; further discussion of these aspects is, therefore, unnecessary.

/ Starch from waxy corn differs from ordinary starch in both molecular structure and pasting characteristics. Pastes made from waxy starch are both translucent and flavorless, whereas pastes from ordinary starch are opaque and have a distinctive flavor (MacMasters and Hilbert, 1944). In addition, waxy starch dextrinizes readily to produce dextrans of high solubility and low viscosity (Schopmeyer *et al.*, 1943). Starch modified by the action of an acid or an oxidizing agent has excellent adhesive strength. The waxy pastes are also characterized by an almost complete lack of retrogradation. Enzyme treatment gives a clear solution, making the pastes particularly valuable for paper coating and textile sizing and finishing. At the present time waxy starch is used primarily in the adhesive and food fields.

2. *Hydrolytic Products*

The hydrolytic products of starch, syrup and dextrose, are more familiar to the general public than some of the modified starches which have been described above. Corn syrup, like the various types of starches, may be produced with a wide variation in properties such as specific gravity and percentage of reducing sugars to meet a corresponding diversity of commercial outlets ranging from tanning of leather and curing of tobacco to the highly refined types which are used in the feeding of infants and for intravenous injections in certain pathological or surgical conditions. No attempt will be made to catalog the properties of these special types or to outline the variations in processing procedures which are necessary for their production.

The refined starch, suspended in water, is placed in large metal tanks or converters where it is hydrolyzed by the action of acid. Increased temperature and pressure are used to hasten the process. The degree of hydrolysis is checked periodically by means of an iodine test; when the desired degree of conversion is attained, the contents of the tank are transferred to a neutralizing tank where the acid is neutralized by the addition of a solution of sodium carbonate. The hydrolytic action is stopped when the liquor contains about 20 to 80 per cent of dextrans, depending upon the type of syrup desired. A certain proportion of dextrans is desired to avoid crystallization in the resulting syrup. The neu-

tralized liquor is either skimmed or filtered to remove any traces of gluten, fatty acids, pentosans, etc., which might impart a cloudy appearance. The liquor is then treated with bone char or some type of activated charcoal to purify and decolor the syrup and finally evaporated under vacuum to the desired consistency. The density of the syrup and the degree of decolorization required depend upon the specific use to be made of the product. Some syrups are prepared in which enzyme conversion follows the usual acid hydrolysis. This process yields a syrup having a greater total sugar content and a lower viscosity. If crystalline dextrose is desired, a somewhat greater quantity of hydrochloric acid is used for hydrolysis and the hydrolytic action is allowed to continue to near completion. The resulting syrup liquors are concentrated to about 40° Bé (Newkirk, 1936, 1939a) and then placed in cylindrical vessels and subjected to slow agitation. The liquor is "seeded" with dextrose crystals of the desired type and held at about 38°C. for several days. The material is then transferred to centrifuges where it is washed free of the mother liquor. The washed crystals, which are then dried, have a purity of 99 to 100 per cent. The mother liquor and wash water are subjected to further treatment to recover additional quantities of sugar. The mother liquor after dextrose has been recovered is marketed under the name "hydrol." It is used in the manufacture of mixed feeds. ✓

The anhydrous form of dextrose may be produced by dissolving the hydrate dextrose after it leaves the centrifuge, treating with an activated carbon, heating, and finally filtering until clear. The filtered liquid is then placed in evaporators and heated until the desired degree of crystallization is attained (Newkirk, 1939b). The mass is then centrifuged and washed as before. Dextrose is used in the manufacture of many confections, in the canning of fruits and vegetables, and in the production of many beverages. ✓

In addition dextrose may serve as source material for a wide range of synthetic organic products such as saccharic and propionic acids and the long-chained alcohols sorbitol and mannitol, to mention only a few. Sorbitol is used in the synthetic production of vitamin C. Mannitol, after nitration, is a good friction-proof detonator (Newkirk, 1939b). 1

Sugars of a lower degree of purity than dextrose are also produced from starch. These are commonly designated as "70," "80," etc., corn sugars, the number referring to the approximate percentage of dextrose. The sugar liquor is cooled and then run onto tables or into forms where it is seeded with sugar crystals and allowed to crystallize. It is then cut into slabs and "cured" to permit maximum crystallization. Such sugars are used in brewing, in the production of viscose rayon, and in the tan-

ning of leather. Most of the caramel color used is produced from corn sugar.

3. Oil

In the outline of the wet-milling operation we considered the germ fraction only through the separation and drying phases. The extraction and purification process will be described below. The oil percentage of the corn kernel varies with the variety and with the cultural, and environmental condition, usually ranging from about 3.5 to 5.0 per cent. In the germ, the oil percentage is much greater, often ranging up toward 50 per cent.

The oil may be recovered from the germ by either an expeller or solvent process. In either case the dried germs are first passed through a series of flaking rolls and then tempered in special drums. In the expeller process the tempered germs are fed into the large end of a tapered barrel. A tapered screw device moves the germ material along the barrel, the taper being responsible for the high pressures which develop. The oil flows out through a special slot and the pressed meal passes out the small end of the expeller. The use of too great pressure results in a darkening of both oil and meal which is undesirable. Therefore, it is undesirable to exert enough pressure to remove all of the oil from the germ. The oil cake often contains 5 to 8 per cent of oil after extraction. The oil recovered amounts to about $1\frac{1}{4}$ to $1\frac{1}{2}$ pounds of oil per bushel of corn.

In the solvent process, the tempered germs are leached by a suitable solvent, usually hexane. After leaching the extracted meal is pressed to remove as much as possible of the oil-solvent mixture, and then the solvent is removed from the oil by distillation. The whole extraction process is carried out in a closed system so that solvent loss is reduced to a minimum. In some cases corn mills may use a combination of both expeller and solvent extraction. The amount of oil remaining in the germ meal after solvent extraction is quite low, usually about 1 per cent.

The oil as it occurs in the corn kernel is made up of a mixture of glycerides. During extraction some of these are broken down into free fatty acids and glycerin. These must be removed, as they are relatively unstable. Several methods may be used in the refining of the oil. In the alkali method the extracted oil is placed in a large tank or vat and treated with a caustic soda solution. The alkali combines with the free fatty acids, the phosphatides, a portion of the coloring matter, and other organic impurities. The saponified materials and glycerin are both soluble in water and may be separated after the oil-water mixture is

allowed to stand. The oil is siphoned off and the residue left is called "soap stock" or "foots." The soap stock may be completely saponified, washed with salt, and then boiled with excess salt. Such soap is used in wool scouring and the production of soap powders. The soap stock may be treated in other ways to recover the free fatty acids and glycerin or may be treated with petroleum ether to recover the phosphatides, of which lecithin is the most important. Lecithin is used in the production of vegetable shortening, margerines, cosmetics, candies, and pharmaceutical preparations.

The oil fraction which is siphoned off is treated with some adsorbent material such as fuller's earth or activated carbon. This treatment removes additional coloring matter and can be controlled so as to ensure uniform coloration in the finished product. The mixture of oil and adsorbent is pumped through filter presses to recover the adsorbent. The oil is heated to about 400°F. and superheated steam blown through it for 3 to 6 hours, after which it is allowed to cool under vacuum. This treatment removes the volatile impurities giving the characteristic odor to the oil. The final step in refining is known as "winterizing." The oil is cooled to about 30°F. and filtered to remove stearin-like materials which may settle out as a fine precipitate. Winterizing need be done only if the oil is to be used for salad purposes.

The refined oil is high in quality and may be used as a cooking or salad oil, in mayonnaise, etc. Corn oil is also used as a solvent for certain drug preparations and considerable quantities are used in the manufacture of rubber substitutes such as factice.

4. *Gluten*

After the steep water has been placed in large tanks and the gluten allowed to settle, the water and dissolved materials are siphoned off. The water content is further reduced by special methods of filtration or by mechanical presses and the solids finally dried to about 12 per cent moisture. The dried product may be used in the production of feed or subjected to further processing for the production of zein, amino acids, etc.

Gluten may be sold for livestock feed in two different forms, gluten feed and gluten meal. Gluten feed contains gluten, hulls, fiber, steep water, and germ. It is usually sold with a guaranteed protein content of about 20 to 25 per cent. Hydrol, the molasses left after sugar has been extracted, may be added to produce a sweetened corn gluten feed. Gluten meal does not contain the additional products, such as hulls, and therefore has an average protein guarantee of about 40 per cent.

Corn gluten may also serve as source material for a number of other

products. The most important of these is zein. Zein is a protein complex which is characterized by its solubility in the short-chain alcohols. However, the alcohol in addition to dissolving zein also dissolves any oil remaining in the gluten and the yellow pigment which has been concentrated in the gluten fraction during milling.

Either ethyl or isopropyl alcohol in high concentration can be used as a satisfactory commercial solvent for zein (Swallen, 1941). The gluten is first ground to pass a 40-mesh screen and then treated with 85 per cent isopropyl alcohol for $1\frac{1}{2}$ to 2 hours at a temperature of 55° to 60°F . The extract contains about 6 g. of protein per 100 ml. and all of the remaining oil and xanthophyll. The solution is cooled to about 15°C . to precipitate any undesirable substances and filtered. The filtrate is mixed with hexane, using about equal proportions of hexane and filtrate. The mixture separates into two layers, the upper layer being largely hexane, oil, and xanthophyll plus a part of the alcohol solvent. The zein remains in the alcohol solvent. The two solvents may be separated by centrifugation. Any hexane remaining in the zein fraction may be recovered by vacuum distillation. The zein is precipitated by spraying into a tank containing agitated refrigerated water. The zein rises to the top and is skimmed off, after which it is washed, filtered, and dried in a flash drier system. Drying must be done rapidly at as low a temperature as possible, since wet zein forms a plastic mass when heated above 15°C .

Zein is used commercially in the production of lacquers, plastics, adhesives, and a textile fiber marketed under the trade name Vicara.

The xanthophyll-oil can be recovered from the hexane solvent and dried (Swallen and Gottfried, 1942). The dried product is used in the preparation of poultry rations.

Gluten may also be used for the production of amino acids, particularly glutamic acid, leucine, and tyrosine.

5. Steep Water

During the 36 to 48 hours that corn is in the steep tanks a certain amount of soluble protein and carbohydrates as well as minerals is removed from the grain. In the early days of the wet-milling industry the steep water, after it had become rich in solubles, was discarded. At a later date this material was disposed of by a partial evaporation and concentration and then added to gluten, fiber, and other fractions and sold as feed. A considerable part of the steep water is still used in livestock feed. More recently a new and important outlet for steep water has been discovered.

At the beginning of World War II the total production of penicillin

was low. Various modifications of culture media were tried in an attempt to increase yields of this substance, but none were markedly successful. A group of workers at the Northern Regional Laboratory at Peoria tried the addition of corn steep water to the culture media and obtained a 10-fold increase in penicillin. Later still greater yields were obtained by using new strains of the penicillium organism. Steep water is also used in the culture solution of other organisms which are grown for the production of antibiotics. The particular ingredient or ingredients of steep water responsible have never been identified or isolated. In fact relatively little is known as to the chemical composition of steep water except in the most general terms.

Steep water is known to contain considerable amounts of two of the B-complex group of vitamins. These are inositol and choline. Inositol is prepared commercially from phytin, a mixed hydrogen-magnesium-calcium salt of inositolhexaphosphoric acid which is found in high concentration in most cereal grains. Choline is a constituent of lecithin and is present in most plant and animal cells. At present these materials are used almost entirely in the field of medicine, but a number of industrial uses may develop.

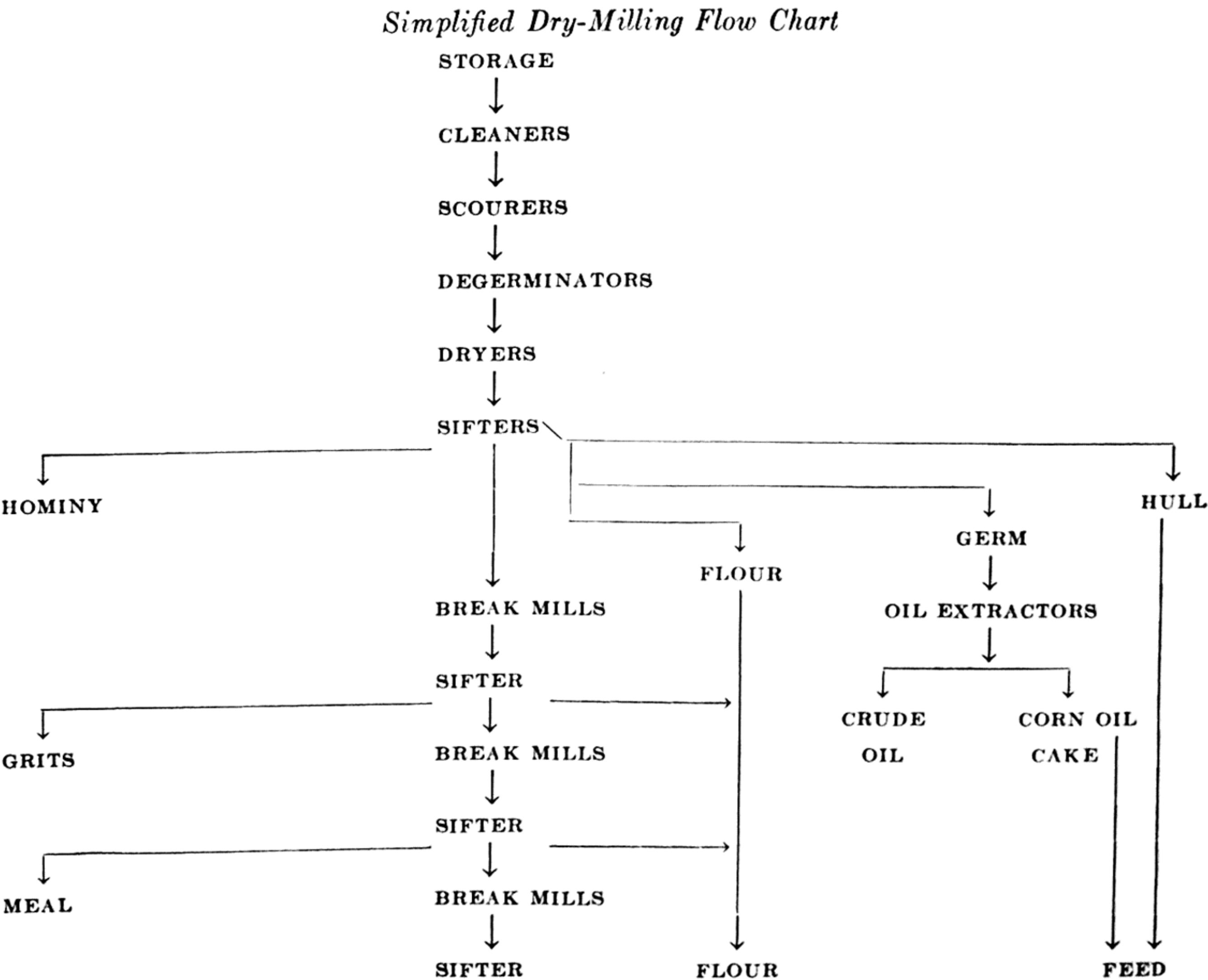
III. Dry Milling

The second largest industrial consumption of corn is by the dry-milling industry. In contrast to wet milling, this process is relatively simple and the products few in number. Basically dry milling involves a physical separation of the corn kernel into its component parts, hull endosperm and germ. The endosperm separate is then graded into various particle sizes, and these are used with a minimum of further modifications (Winton *et al.*, 1915).

The first step in milling, after the grain is cleaned, is tempering. The corn is brought to a moisture content of about 20 per cent by means of a water spray or steam. Since this is done rapidly, there is a marked difference in moisture percentage in various portions of the kernel. This unequal distribution of moisture is of decided advantage in the next phase of the milling operation. The tempered corn is fed into a Beal degerminator. This machine consists of a tapered horizontal drum revolving inside a casing of the same shape. The opposing surfaces of the drum and casing are studded with cone-shaped projections about $\frac{3}{4}$ inch long. The clearance between drum and casing can be adjusted while the machine is in operation. The normal clearance is about $\frac{7}{16}$ inch. The inner drum revolves at a speed of about 700 r.p.m. The corn enters at the narrow end of the machine and is carried through the length of the revolving core. The impact of the corn against the projec-

tions tends to loosen both the hull and the germ with a minimum of grinding of the endosperm. The finer particles escape through perforations, and the coarse material is discharged at the large end of the drum. The bran and germ may be partially removed at this stage by suction. The broken corn may be partially dried and passed through a hominy reel. This is essentially a revolving slotted cylinder. Within the cylinder a beater revolves in the opposite direction. The hominy reel separates the bran and feed stock meal from the germ. The endosperm material passes through a sizing reel which removes all of the fine material. Aspiration removes further amounts of bran and flour. The coarse endosperm material is next passed through a series of three break rolls, being screened and aspirated after each break to separate flour, meal, fine grits, coarse grits, and hominy.

The oil is removed from the germ fraction by the same process as in wet milling. However, because of the less efficient germ separation the amount of oil recovered per bushel of corn is only about one-third to one-half that obtained by the wet process. The unrefined oil from the dry process tends to be somewhat lower in fatty acids than oil from the wet process (Sievers, 1920; Sievers and Shrader, 1922).



The endosperm particles of largest size (pearl hominy) are usually cooked with malt before flaking. The flaked particles may then be toasted to produce corn flakes or if left untoasted are called brewers' flakes, foundry flakes, paper hangers' flakes, etc. Brewers' flakes and grits of various sizes are used in the brewing industry. Grits and meal are used extensively for human consumption. These products prepared from white corn are preferred in the South, whereas yellow products are commonly preferred in the North. For some time it was thought that corn flakes could be made only from white corn. However, yellow corn is now used extensively in the production of this breakfast cereal.

In ordinary milling practices corn flour is produced in quantities equal to about 5 per cent of the corn kernel. Corn flour is used as an ingredient in pancake mixes, as a filler or binder in various meat products, and as a substitute for wheat flour.

IV. Fermentation Industries

The principal raw materials of the fermentation industries are starch and sugar. In the discussion of fermentation and its products which follows, corn, or its by products starch and sugar, may be used as the parent material. However, since starch and sugar are available from many sources, corn is used as a preferred source only when the price relationship is favorable.

Some indication of the possible scope of the fermentation industries is afforded by the following list of substances which may be produced from either starch or dextrose by the action of one or more microorganisms (Fulmer and Werkman, 1930). This list is as follows: acetaldehyde, acetic acid, acetone, acetylmethyl carbinol, butyl alcohol, 2,3-butyleneglycol, butyric acid, caproic and caprillic acids, citric acid, ethyl alcohol, formic acid, fumaric acid, gluconic acid, glycerol, lactic acid, oxalic acid, oxygluconic acid, propyl alcohol, pyruvic acid, and succinic acid. If one or more of the above substances were used as substrates for further fermentation, the list of possible products could be extended materially.

The production of ethyl alcohol is undoubtedly the oldest and is still the most important of the many fermentation products. Important advances have been made in recent years in the economy of the procedures used in the production of alcohol.

The production of alcohol from corn may involve different milling and saccharification processes. The simplest type of milling is merely to grind the whole corn. The corn may also be ground by either the dry- or wet-milling process to facilitate oil recovery. The ground corn or starch is mixed with water and then gelatinized by cooking at tempera-

tures ranging from 240° to 310°F. This resulting "mash" is saccharified by conventional malting methods, by the diastatic action of molds, or by acid hydrolysis. Of the three methods acid hydrolysis appears to be the least desirable because of the equilibrium between dextrose and polysaccharides. Some of these polysaccharides cannot be converted to alcohol by enzymatic action. The choice between malt and mold diastatic conversion will depend upon the use to be made of the alcohol. If the alcohol is to be used for beverage purposes the use of malt diastase is preferred. Malt equal to about 8 to 10 per cent of the weight of the corn is required for satisfactory saccharification. However, the yield of alcohol following mold conversion is somewhat more efficient (Underkofler *et al.*, 1939). The cost of the "mold" powder is also somewhat less than the cost of malt when allowance is made for the quantities required for saccharification of the given weight of corn.

After saccharification by any of the above three methods the solution is acidified to the optimum pH and inoculated with a liquid suspension of growing yeast cells. The usual method for preparing yeast cultures for inoculation of the fermentation vats in a grain alcohol plant involves the following general steps: (1) withdrawal of plant grain mash into yeast tubs, (2) addition of supplemental malt, (3) inoculation with and growth of lactic acid bacteria to increase acidity, (4) sterilization by heating, (5) inoculation with yeast, and (6) growth of the yeast culture (Underkofler, Severson, and Goering, 1946). The enzyme zymase from the growing yeast cells converts dextrose to ethyl alcohol.

Complete fermentation requires from 30 to 90 hours. The concentration of alcohol in the solution or "beer" varies with the original sugar concentration, temperature, and the efficiency of the enzymatic action but normally varies from 6 to 8 per cent by volume. The beer is then pumped to a beer still or stripping column where the alcohol and an approximately equal quantity of water are removed by distillation. The 50 per cent alcohol is rectified to about 95 per cent by fractional distillation.

This fractionation may be used to effect as many separations as desired simultaneously. The most volatile separates include a mixture of acetaldehyde and ethyl alcohol. The next less volatile separate, which may include several grades, is composed primarily of ethyl alcohol and water. The alcohol is usually recovered at about 95 per cent concentration by volume. A still less volatile fraction includes ethyl alcohol and other higher alcohols, of which amyl alcohol is present in greatest concentration. Other components—fusel oil, water, and mash residue—remain in the fractionating still.

Anhydrous ethyl alcohol may be obtained by the distillation of a mixture of the 95 per cent alcohol and some suitable solvent such as benzene. This distillation yields three products: (1) a tertiary mixture of water, alcohol, and benzene, (2) a binary mixture of alcohol and benzene, and (3) absolute alcohol. Dilution brings about a separation of the benzene, which can be recovered.

Large quantities of industrial alcohol were produced by fermentation of carbohydrates during World War II. The synthetic production of ethyl alcohol has become of increasing importance in recent years. If this trend continues, it may well be that the production of alcohol from corn may be limited to the production of beverage alcohol.

The production of beverage alcohol follows the same general pattern as that outlined for industrial alcohol. The main difference lies in the treatment following rectification. The distilled spirits, about 95 per cent alcohol by volume, are filtered through charcoal or activated carbon and aged in charred oaken casks. This type of storage imparts the desired flavor and color to the product.

1. *Distillers Grains*

The stillage (mash residue remaining after the removal of alcohol) represents the only important source of waste from a distillery operating on cereal grains. This may be used as a livestock feed without drying and is then known as distillers slops. This material is too bulky for transportation and, therefore, the bulk of the stillage is processed and dried.

The wet material is first screened and the screenings pressed and dried to produce "light distillers grains." The screened stillage is concentrated by evaporation to 25 to 50 per cent solids. These may be mixed with the pressed screenings and dried to produce "dark distillers grains" or dried on drum driers to give distillers dried solubles. These dried solubles constitute a valuable supplement to poultry and swine rations (Boruff, 1947).

2. *Butylene Glycol*

Several organisms are capable of fermenting dextrose or starch to produce a mixture of 2,3-butylene glycol and ethyl alcohol (Christensen, 1944). Some of these, such as *Clostridium polymyza* and some strains of *Aerobacter aerogenes* produce sufficient amylase so that they may act on starch without saccharification. Other strains of *Aerobacter aerogenes* produce only limited amounts of amylase, and the starch must be saccharified to complete fermentation in a reasonable period of time.

When *Clostridium polymyza* is used as the fermenting organism, a mixture of butylene glycol and ethyl alcohol is produced in the approximate ratio of 1.5–2.0/1, respectively. If *Aerobacter aerogenes* is used, the fermentation yields *meso*-glycol, and variable amounts of lactic acid and ethyl alcohol. The amounts of these two substances can be held to low levels by proper control of sugar concentration, pH, and minerals. If ground grain has been mashed, the recovery of butylene glycol from the stillage presents a definite problem. Recovery is normally accomplished by extraction with a solvent such as *n*-butyl alcohol or ethyl ether.

The problem of recovery of glycol may be simplified materially by using starch rather than ground whole corn as the substrate. Kooi, Fulmer, and Underkofler (1948) have shown that unsaccharified corn starch may be fermented by *Aerobacillus polymyza* to produce satisfactory yields of 2,3-butanediol (2,3-butylene glycol). The yields, in terms of starch fermented, were 26.8 per cent butanediol, 1.1 per cent acetyl-methyl carbinol, and 14.8 per cent ethyl alcohol. The separation of the butylene glycol is much easier than when saccharified mash is used. In addition the wet-milling by-products such as gluten and oil resulting from the starch separation are recovered by the standard procedure.

3. Butyl Alcohol-Acetone

In an earlier section on the production of ethyl alcohol it was mentioned that fusel oils were recovered during fractional distillation. One of the components of fusel oil is *n*-butyl alcohol. However, the butyl alcohol recovered as a by-product of ethyl alcohol fermentation is far short of industrial demands.

The butyl alcohol-acetone fermentation process is an outgrowth of earlier work done in England on synthetic rubber. It was decided that the most feasible process was by polymerization of isoprene or butadiene. The most feasible way to prepare these in turn was thought to be from isoamyl and butyl alcohol, respectively. Prior to this time Fernbach of the Pasteur Institute had isolated a mixture of bacteria which were able to act directly upon potato starch to produce amyl alcohol. Later Weizmann working at the University of Manchester isolated a different type of bacterium which was able to ferment starch from cereals as well as potatoes without preliminary treatment. This fermentation was characterized by the production of much larger quantities of acetone than was characteristic of the bacterial mixture used in the earlier studies. Shortly after this development World War I broke out, and acetone was in great demand for the production of the explosive cordite.

Consequently, the Weizmann process was put into extensive use. With this process the final products of fermentation are *n*-butyl alcohol, acetone, and ethyl alcohol in the approximate proportions of 6/3/1, respectively (Gabriel and Crawford, 1930).

The process involves the use of either whole corn or degerminated corn which has been ground to a meal. The meal is made into a slurry containing about 6 to 8 per cent of meal by weight and cooked at about 30 pounds pressure for 2 hours. The cooking serves to produce a uniform paste and also to sterilize the material. After cooling the slurry is placed in closed fermentation tanks and inoculated with a strain of *Clostridium acetobutylicum*. Fermentation is complete at the end of two to three days and the fermentation products recovered by fractional distillation. The butyl alcohol is converted to butyl acetate and used as a solvent in the production of nitrocellulose lacquers.

CO₂ and hydrogen are commonly recovered during the course of fermentation. The hydrogen and a part of the CO₂ are used for the synthetic production of methanol and the remainder of the CO₂ used to produce dry ice.

4. Lactic Acid

A fermentable sugar such as glucose may be used for the production of lactic acid. In addition to the sugar a supply of nitrogen and inorganic salts must be present for the proper growth of the bacteria *B. Delbruckii* or some species of *Lactobacillus*. Gluten from the wet-milling process is often used as the nitrogen source.

Calcium carbonate is added at the beginning of the fermentation process to neutralize the lactic acid as rapidly as it is formed. An excess of lactic acid retards or inhibits the fermentation process. Several days are required for complete fermentation; after completion the calcium lactate is treated with sulfuric acid to form lactic acid and calcium sulfate. The calcium sulfate is separated by filtration. The weak lactic acid solution (about 8 per cent) is concentrated in vacuum pans. The bulk of the lactic acid produced is of the "technical" grade. If it is to be used for edible purposes it must be subjected to additional refining and purification.

The edible grades of lactic acid are used in a wide variety of food and beverage products as well as livestock fields. The nonedible technical grades of lactic acid are used in the dyeing and finishing of textiles and in the production of ethyl lactate, a solvent for nitrocellulose in the production of lacquers. However, the bulk of the lactic acid produced is used in the processing of leather. In this connection, it is used to remove lime from dehaired hides and also in the plumping of leather.

5. Glycerol

Yeast acting on dextrose or other fermentable sugars produces ethyl alcohol and only small quantities of glycerol if the media is normal or slightly acid. However, if the media is made alkaline or if sodium sulfate is added, the proportion of these two products is reversed and glycerol is the predominant product (May and Herrick, 1930). The procedures outlined under alcohol with respect to grinding, saccharification, and inoculation with yeast, therefore, are common to both ethyl alcohol and glycerol fermentations.

6. Acetic Acid

Table vinegar is commonly made from the juice of apples. However, it can be made from other fruits and from honey. Corn sugar has also been used to produce an acceptable white vinegar.

After the fermentable sugar has been converted to alcohol and carbon dioxide by the action of yeast, the alcohol may be broken down by the action of bacteria (*Bacterium aceti*) to produce acetic acid. It is believed that acetaldehyde is an intermediate step in this conversion. In fact, if insufficient aeration is provided the reaction will stop with the formation of acetaldehyde.

The process commonly used for the production of vinegar is to allow the alcohol solution to trickle down over wood shavings previously inoculated with the acetic bacteria.

REFERENCES

- BARTLING, F. W. 1940a. Wet process corn milling No. 5. The steephouse. *Am. Miller* **68**: (No. 8): 40-41, 82.
- BARTLING, F. W. 1940b. Wet process corn milling No. 6a. The mill house. *Am. Miller* **68** (No. 12): 28-30, 84-85.
- BARTLING, F. W. 1941a. Wet process corn milling No. 6b. The mill house. *Am. Miller* **69** (No. 2): 32-34, 89-90.
- BARTLING, F. W. 1941b. Wet process corn milling No. 7. The table house. *Am. Miller* **69** (No. 5): 34-36, 104-105.
- BARTLING, F. W. 1941c. Wet process corn milling No. 8. Filtering, washing and refining tabled starch. *Am. Miller* **69** (No. 8): 40-44, 81-82.
- BARTLING, F. W. 1942. Wet process corn milling No. 8. Drying corn starch. *Am. Miller* **70** (No. 2): 38, 43, 82, and 83; (No. 3): 80-81; (No. 8): 46-47, 85.
- BARTLING, F. W. 1943. Wet process corn milling No. 12. The refining building. *Am. Miller* **71** (No. 8): 56, 58, 71, 88, 90; (No. 11): 50, 51, and 59.
- BARTLING, F. W. 1944. Wet process corn milling, production of corn syrup. *Am. Miller* **72** (No. 2): 64, 66, 72.
- BORUFF, C. S. 1947. Recovery of Fermentation residues as feeds. *Ind. Eng. Chem.* **39**: 602-607.

- CHRISTENSEN, L. M. 1944. Use of starch and starch products in the fermentation industries. in "Chemistry and Industry of Starch, Starch Sugars and Related Compounds" (R. W. Kerr, ed.), pp. 366-377. Academic Press, New York.
- COX, M. J., MACMASTERS, M. M., and HILBERT, G. E. 1944. Effect of the sulfurous acid steep in corn wet milling. *Cereal Chem.* **21**: 447-465.
- FULMER, E. J., and WERKMAN, C. H. 1930. "An Index to the Chemical Action of Microorganisms on the Non-nitrogenous Compounds," 198 pp. Charles C Thomas, Baltimore, Maryland.
- GABRIEL, C. L., and CRAWFORD, F. M. 1930. Development of the butyl-acetone fermentation industry. *Ind. Eng. Chem.* **22**: 1163-1165.
- GARRETT, J. F. 1930. Lactic acid. *Ind. Eng. Chem.* **22**: 1153-1154.
- HIXON, R. M., and SPRAGUE, G. F. 1942. Waxy starch of maize and other cereals. *Ind. Eng. Chem.* **34**: 959-962.
- KERR, R. W. 1944. "Chemistry and Industry of Starch, Starch Sugars and Related Compounds." Academic Press, New York.
- KOOI, E. R., FULMER, E. I., and UNDERKOFER, L. A. 1948. Production of 2,3 butanediol by fermentation of cornstarch. *Ind. Eng. Chem.* **40**: 1440-1445.
- MACMASTERS, M. M., and HILBERT, G. E. 1944. Glutinous corn and sorghum starches. *Ind. Eng. Chem.* **36**: 958-963.
- MAQUENNE, L., and ROUX, E. 1905. Sur la constitution, la saccharification et la retrogradation des fe'cule. *Compt. rend.* **140**: 1303-1308.
- MAY, O. E., and HERRICK, H. T. 1930. Some minor industrial fermentations. *Ind. Eng. Chem.* **22**: 1172-1176.
- MEYER, K. F., BRITANO, W., and BERNFIELD, P. 1940a. Recherches sur l'amidon II Sur la nonhomogeneite de l'amidon. *Helv. Chim. Acta* **23**: 845-853.
- MEYER, K. F., BERNFIELD, P., and WOLFF, E. 1940b. Recherches sur l'amidon III Fractionnement et purification de l'amylose de maizé naturel. *Helv. Chim. Acta* **23**: 854-864.
- MEYER, K. F., and BERNFIELD, P. 1940c. Recherches sur l'amidon V l'amylopectine. *Helv. Chim. Acta* **23**: 875-885.
- NEWKIRK, W. B. 1936. Development and production of anhydrous dextrose. *Ind. Eng. Chem.* **28**: 760-766.
- NEWKIRK, W. B. 1939a. Hydrate dextrose. *Ind. Eng. Chem.* **31**: 18-22.
- NEWKIRK, W. B. 1939b. Industrial use of starch products. *Ind. Eng. Chem.* **31**: 153-157.
- NEWTON, J. M., and PECKHAM, G. T., JR. 1944. Oxidation of starch. Ch. XI in "Chemistry and Industry of starch, starch sugars and related compounds" (R. W. Kerr, ed.). Academic Press, New York.
- RADLEY, J. A. 1943. "Starch and Its Derivatives," 2nd ed., 558 pp. Chapman and Hull Ltd., London.
- SCHOCH, T. J. 1941. Physical aspects of starch behavior. *Cereal Chem.* **18**: 121-128.
- SCHOPMEYER, H. H., FELTON, G. E., and FORD, C. L. 1943. Waxy cornstarch as a replacement for tapioca. *Ind. Eng. Chem.* **35**: 1169-1172.
- SIEVERS, A. J. 1920. The production and utilization of corn oil in the United States. *U.S. Dept. Agr. Bull.* **904**, 1-22.
- SIEVERS, A. J., and SHRADER, J. H. 1922. The production of an edible oil from crude corn oil. *U.S. Dept. Agr. Bull.* **1010**, 1-25.
- SWALLEN, L. C. 1941. Zein—a new industrial protein. *Ind. Eng. Chem.* **33**: 394-398.
- SWALLEN, L. C., and GOTTFRIED, 1942. Purification and uses of xanthophyll oil derived from corn. *Oil and Soap* **19**: 58-59.

- UNDERKOFER, L. A., SCHOENE, L., and FULMER, L. E. 1939. Saccharification of starchy grain mashes for the alcoholic fermentation industries. *Ind. Eng. Chem.* **31**: 734.
- UNDERKOFER, L. A., SEVERSON, G. M., and GOERING, K. J. 1946. Saccharification of grain mashes for alcoholic fermentation. *Ind. Eng. Chem.* **38**: 980-985.
- WINTON, A. L., BURNETT, W. C., and BORNMANN, J. H. 1915. Composition of corn (maize) meal manufactured by different processes and the keeping qualities. *U.S. Dept. Agr. Bull.* **215**, 1-31.

CHAPTER XV

The Nutritive Value of Corn

BURCH H. SCHNEIDER

I. Introduction

The chief properties of grains are their relatively high contents of energy and low percentage of proteins, the latter being of rather poor quality. Grains are the principal concentrates, others being by-products of industrial processes. Concentrates can be defined as feeds that are rich in energy and are highly digestible. Home-grown grains are the cheapest sources of concentrates to the farmer and stockmen, except when demand for grain for human food or government price support makes the price too high to use it for livestock (as is true of wheat). Grains, properly fed, result in greater milk yield from dairy cows and more marketable carcasses in meat animals, and are required by draft or pleasure horses for prolonged work or great speed.

In addition to their protein deficiencies, the only vitamins which grains contain in significant amounts with any consistency are thiamine and vitamin E. Yellow corn is unique in that it supplies vitamin A to animals. Some of the B-complex vitamins are present in the different grains in variable amounts. The grains supplement the forages by supplying energy. Also, they add somewhat more phosphorus but much less calcium to rations than do the common forage crops. When grains are fed to cattle, sheep, or horses with sufficient legume roughages, there is usually enough protein and calcium, and a fairly satisfactory ration results.

II. Corn

In the United States, corn is used primarily for animal feeding. In other lands it is more a source of human food. In the southeastern states, it is used more for the people's diet than elsewhere in the United States. About four-fifths of the corn produced in the United States is consumed in livestock feeding. It is important as a livestock feed throughout North America because it is produced in such surplus in the Mississippi Valley. It is often "a good buy" thousands of miles away, where it must compete with locally produced crops. In any case, the price of corn

always affects the price of all other feeds. When corn is plentiful and cheap, it will tend to give lower prices for comparable feeds, i.e., the other cereals. In the Corn Belt, livestock feeders cannot afford not to feed it; however, they must understand its nutritive value if they are to use it wisely. Even those who live at great distances from the center of production, or who may attempt to grow corn in less favorable environments, should be well informed regarding its nutritive value.

Corn most completely demonstrates the better qualities and efficiencies of the feed grains. Corn is among the highest in net energy content, lowest in protein, and lowest in fiber content. It, as much as any of the grains, justifies the name "concentrate" because of the condensed form of its nutrients. Animals like it and eat it readily.

III. Differences in Corn

Yields of *dent* corn have increased considerably because of the development of hybrid varieties. The first hybrids released for commercial production tended to be harder than open-pollinated corn. Thus, hybrid corn has about 3 per cent less feeding value than open-pollinated corn (Robison, 1939, 1944). This fact is usually overlooked because of the greater yield of the hybrids.

Hybrid dent corn is not so hard and hornlike as *flint* corn but has essentially the same chemical analysis. Dent corn, since it is softer, has slightly greater feeding value. *Waxy* corn, for milling into tapioca, is less palatable, but otherwise appears fully as valuable as a feed as the usual dent corn.

Sweet corn is normally grown for human food and sold as an immature fresh crop. When mature, it contains a very hard starch instead of the sugar of the immature kernel. Since it contains higher percentages of protein and fat, it might appear to be a good livestock feed. However, because the yield of sweet corn is not so great as that of dent corn, it has not been developed as a livestock feed.

Popcorn kernels are even harder than any of the other types of corn which have been discussed. They are high in protein and fat. Popcorn can be fed to livestock but must always be ground because of its hardness.

IV. Chemical Composition

The first consideration in estimating the nutritive value of any livestock feeding stuff or human food is its chemical composition. This classification by chemical means is stated first in terms of the traditional feed analysis or proximate analysis, averages of which are shown in Table I. The average mineral constituents contained in the ash are

shown in Table II. The average vitamin content of corn is shown in Table IV.

The variations in these nutrients in corn (not given herein) are shown in two of the original sources of data listed in Tables I, II, and IV. In the study of corn by the Committee on Feed Composition of the National Research Council (Schneider *et al.*, 1953a, b), the 95 per cent confidence limits, the standard deviations, and the coefficients of variation for the data are presented. In this survey, every effort was made to observe the best of sampling techniques and to obtain corn from states and counties in proportion to their production. This was necessary to

TABLE I
THE PROXIMATE COMPOSITION OF CORN (85% DRY MATTER)

	<i>Corn^a</i> <i>analysis</i> <i>avg. 1910</i> <i>& 1911</i>	<i>From^b</i> <i>digestion</i> <i>studies</i>	<i>National Research^c</i> <i>Council Report No. 2</i> <i>1946</i> <i>1947</i>	
Crude protein, %	8.34	9.29	8.66	9.08
Fat (ether extract), %	3.46	3.97	3.89	3.86
Crude fiber, %	1.85	2.03	1.99	2.07
N-free extract, %	69.79	68.35	69.22	68.71
Ash, %	1.56	1.37	1.225	1.271
Energy, Cal./g.	—	3.81	3.864	—

^a Four cargoes of North American dent corn loaded for export. Chemical analysis of the individual samples made by Cattle Food and Grain Laboratory of the Bureau of Chemistry, United States Department of Agriculture (Daugherty, 1914).

^b Schneider (1947 and unpublished data). These are analyses of 81 samples of corn fed in digestion trials in the United States and abroad from 1876 to 1943. The Cal./g. were determined on only 36 of these samples.

^c Schneider *et al.* (1953a, b).

accomplish the goal that the sample means be representative of the entire crop of the United States. Beeson (1941) shows the range of values for each element given in his extensive compilation.

These differences raise the question of why the composition of a feed varies. What other than fortuitous reasons cause the amount of a nutrient to be high or low in a feed? Sometimes these variations are significant and large, sometimes not. In the National Research Council Committee study, the protein content of corn was lower than average in Illinois, Indiana, Ohio, Kentucky, West Virginia, and Tennessee. This low protein level, averaging only 8.54 per cent, appeared to extend southward and southwestward to include Georgia, Alabama, Mississippi, Arkansas, and Texas. Corn of about average protein content was obtained in Minnesota, Iowa, Missouri, New York, and Pennsylvania. These states averaged 8.80 per cent protein, whereas the average of all

analyses was 8.84 per cent. Corn of above-average protein content was obtained in North Dakota, Nebraska, Kansas, Oklahoma, Wisconsin, Michigan, and on the Atlantic Seaboard from New Jersey to South Carolina. These averaged 9.50 per cent protein.

The fat content of corn likewise varied somewhat. The lowest fat content was found in Indiana, Ohio, Kentucky, and West Virginia. This corresponds approximately to the low-protein states except that Illinois and Tennessee are not included. Also, the southern states which appeared to produce corn slightly lower in protein, did not fall in the low-fat states. Instead, the southern states including Texas and Oklahoma seemed to produce corn of higher than average fat content. The same was true of some of the states in the East and Midwest.

Generally, the southern states supplied samples having less iron than those from the Midwest or northern and eastern states. In these studies location and variety of corn were confounded, so perhaps some of these geographical differences may be attributed to color or variety. In many ways variety of corn is a function of climatic regions.

The fat of corn was the only nutrient which appeared to have a substantial correlation with the Great Soil Groups classification. There was only very slight relationship between the mineral content of corn and soil classes.

In both years of this study, the fat percentage of white corn was higher and the iron percentage lower than for yellow corn. However, the most important difference between white and yellow corn was in the carotene content. Between the varieties of yellow corn, the only significant difference appears to be in fat percentage.

The effects of various factors on the composition of corn have been studied extensively. Aurand *et al.* (1950) and Doty *et al.* (1943) have investigated the effects of heredity on chemical composition of corn. Weeks and Fergus (1946) investigated the effects of soil, soil treatment, seasonal variation, and variety on the composition of corn. Although all of these factors are important, from the viewpoint of this chapter the effect of these factors on the nutritive value of corn is more important.

V. Moisture Content of Corn

1. Soft Corn

By far the greatest difference in nutrient composition of corn is caused by moisture differences. Corn perhaps varies in this respect more than any other grain. This is evidenced by the various grades of corn, which are based largely on the moisture content. In the National Research Council survey, 1947 was a "soft corn year." However, these

and other studies indicate that the dry matter of corn may not be significantly different chemically or in nutritive value because of variations in water content (Johnson *et al.*, 1943).

It is a common occurrence, wherever corn is grown extensively, to have a crop of soft corn (corn high in moisture or that is immature) every few years. Many farmers try to raise the most productive varieties which require the maximum growing season for their area. One of the biggest problems affecting the feeding of such corn is its proper storage. It must be fed to livestock if it is used at all, for it cannot be handled readily in commerce unless it is dehydrated. Johnson *et al.* (1943) favored piling such corn in long ricks. Rusk and Snapp (1928) recommended keeping soft corn in a silo. Bechtel *et al.* (1945) found that they could store soft snapped corn, either chopped or unchopped, in pits 4 feet in diameter and 5 feet deep, lined with one thickness of burlap sacking to reduce soil contamination. The corn was well packed and water was added. Recommendations developed at the Iowa State College (Anonymous, 1945) suggested the use of a trench silo and advised that the corn be left in the field as long as possible, that temporary cribs be built away from buildings where the wind will hit them, or that ventilator shafts be built through the middle of wider corn cribs.

Shedd (1945) found that it would take from two to four months for corn containing 45 to 65 per cent moisture to dry down to 15 to 25 per cent moisture. In addition to ensiling the entire corn plant, or the ears, he discussed cutting and shocking the fodder. Both shocking fodder or cribbed soft corn have serious disadvantages and may result in badly spoiled corn unfit for feeding. Rusk and Snapp (1928) (Anon., 1924) showed that the ear corn silage could be stored as well as normal silage made from the entire corn plant. They concluded that the feeding value of the dry matter in well-preserved soft corn is equal to that in sound mature corn.

Some studies (Robison, 1922, 1944) indicated that immature corn high in moisture is equivalent to dried corn when expressed on an equal dry matter basis. Others rate it somewhat lower. Wilson and Bushey (1926) found that soft corn puts a good finish on cattle. Also, they noted that the husks on immature snapped corn had considerable feeding value. Steers fed snapped corn and alfalfa hay made better gains than similar animals fed husked corn from the same field. Johnson *et al.* (1943) demonstrated that soft ear corn could be used for feeding swine, beef cattle, or lambs. Pigs fed dry hard corn made faster gains, but the difference was not great and was of doubtful significance. Yearling steers and calves fed soft corn gained faster than those fed

hard corn. The shrink at marketing time with steers fed soft corn was no greater than with those fed hard corn. The hard corn lambs fed out-gained the soft-corn lambs significantly, but those on soft corn did surprisingly well.

Heidenreich and Wilson (1952) differentiated between mature and immature soft corn, pointing out that previous work at the same experiment station (South Dakota), although with corn high in moisture, had been with mature corn. These workers found that about 25 per cent more dry matter from artificially dried *immature* soft corn was required than the dry matter from the same corn fed to pigs in a wet state. With pigs, shelled corn and artificially dried immature shelled corn gave daily gains of 1.86 pounds and 1.73 pounds per head, respectively. These were significantly greater than the 1.52 pounds per head daily gain obtained with hand-fed wet immature ear corn containing about 50 per cent moisture in the kernels.

One of the pertinent points with regard to moisture content of corn is its influence on the feed texture and its acceptance by animals. Carlson and Hoelzel (1949) found that soaking dry corn kernels increased the amount that rats would consume. Robison (1944) found that pigs often choose the dryer of two corns.

2. *The Grades of Corn*

The federal grades of corn are determined by the moisture content, the test weight per bushel, the foreign material in the corn, and the proportion of unsound kernels (U. S. Dept. Agr., 1934). The price at central markets is based on the grade. No. 1 grade contains 14 per cent or less moisture, No. 2, 15.5 per cent, No. 3, 17.5 per cent, No. 4, 20 per cent, and No. 5, 23 per cent. Sample grade corn is that containing greater than 23 per cent moisture. The grade of corn is influenced by the weather conditions before it is harvested, because those conditions influence the maturity and the dryness of the crop. Usually, ear corn poorer than No. 4 grade cannot be stored for feed safely without being chopped and put in a silo. Newly harvested corn cannot be stored as shelled corn early in the season unless it approaches No. 1 grade. It should not be ground except in small quantities for a few days at a time, as fed, unless it is very dry. Ground corn mixed with other bulkier feeds will not mold or become rancid so rapidly as unmixed corn.

VI. The Protein Content of Corn

1. *Quantity of Protein*

J. E. Hunter (unpublished data) has called attention to the fact that to raise the amount of protein in U. S. mixed feeds that would

normally be supplied by corn by 1 per cent would require over 2 million tons of soybean oil meal or its equivalent. Stated thus, the percentage of protein in corn becomes of great financial as well as nutritional importance. Corn requires more protein supplement than any of the other grains in feeding all classes of livestock.

In commercial production, high yields of corn per acre tend to give corn that is lower in percentage of protein. This effect has been alleged to be a result of the widespread use of hybrid seed corn. However, this tendency is not inherent in hybrid corn (Aurand and Miller, 1949), since certain strains have been developed that contain up to 20 per cent or even more of crude protein, with adequate nitrogen fertilization of the soil. However, it appears that the varieties having more than 12 per cent protein do have somewhat lower yields per acre.

Ross *et al.* (1952) fed three lots of lambs on rations containing timothy hay, molasses, and corn containing 7.72, 11.03, and 13.2 per cent crude protein, respectively. The low-protein corn produced significantly lower gains and less wool than the other two groups. There was no significant difference between the weight gains or the wool produced by the lambs receiving the corn containing 11.3 per cent and 13.2 per cent protein. This experiment in which the amount of protein was a limiting factor was a clear demonstration of the importance of the protein content of corn.

2. Quality of Corn Protein

Not only is the quantity of protein in corn important but its quality is also. Different varieties of corn have significant differences in the qualities of their protein, as shown by Myburgh (1946). In addition to this, as the amount of protein in corn increases it is believed that an increasing proportion is made up of zein, a low-quality protein. The entire protein in corn is known to be low in quality, because it is deficient in lysine and tryptophan. However, the germ protein is much higher in quality (Mitchell and Beadles, 1944). Thus, it is assumed that as the amount of protein is increased through corn breeding, the quality of its protein becomes increasingly inferior. Using isocaloric diets with rats and with swine, Dobbins *et al.* (1949, 1950a) concluded that this difference in protein quality between high- and low-protein corn is not significant for growth. However, all levels of protein in corn are of inferior quality. A better quality of protein should be supplied with corn, no matter whether it is of high or low protein content. Such a protein supplement, according to the early workers Osborne and Mendel (1914) and later Hogan (1916) and Marias and Smuts (1940), should be high in both lysine and tryptophan. Dobbins *et al.* (1950b) found that the protein of low-protein corn had a higher biological value.

Hamilton *et al.* (1951) investigated corn produced on land that had grown corn continuously for 70 years without fertilization. The kernels were 26 per cent smaller than those from the comparable fertilized plots and the germ occupied 17 per cent less of the kernel than in normal corn. For this reason, the oil and phosphorus contents were both below normal. Protein was 30 per cent below normal, but nicotinic acid was virtually unchanged. The corn on fertilized or rotation plots in these experiments produced normal grain, although the protein was of poorer quality because of the higher proportion of zein, causing lysine and tryptophan to be a relatively lower proportion of the total protein.

This tendency for the quality of protein to be lower and the zein content to be higher as the quantity of protein is increased is shown also by the work of Mitchell *et al.* (1952), Schneider *et al.* (1952), Shawalter and Carr (1922), Frey (1949, 1951), Hansen *et al.* (1946), Sauberlich *et al.* (1953a, b).

It is reasoned by Frey *et al.* (1949) that the best way to improve the nutritive value of the protein part of corn would be to increase its tryptophan content instead of selecting for a higher total protein level. By mating selected parent stocks it was found possible to increase the tryptophan content of corn by 12.7 per cent. Frey (1951) found that the yield of grain per plant is negatively correlated with the percentage of protein. He also concluded that as the protein becomes higher the zein content of corn increases, thus causing a poor-quality protein, tryptophan and valine are decreased, leucine is increased, but isoleucine is unaffected. Valine, leucine, and isoleucine were closely related but none was correlated with tryptophan content. The above conclusions relating to tryptophan were contrary to those of Miller *et al.* (1950), who believed that tryptophan varied directly with the crude protein content of corn. Frey (1951) concluded that the protein of high-protein corn appears to be less nutritionally adequate than that of low-protein corn because the latter has relatively less zein. Creveaux-Bourgeat *et al.* (1949) in experiments with rats fed a diet of equal parts of corn and wheat reported that the addition of 0.5 per cent DL-tryptophan gave no more growth than no addition at all, whereas a hydrolyzate of casein with or without any tryptophan gave equal and much greater growth. Eggert *et al.* (1951) in nitrogen balance trials with pigs verified that corn having a higher percentage of protein was more deficient in lysine and/or tryptophan than corn containing a lower level of protein.

Some years ago Morrison, Bohstedt, and Fargo (1923) devised the Wisconsin Trio Mixture consisting of 50 per cent tankage, 25 per cent linseed oil meal, and 25 per cent chopped alfalfa to supplement corn as

the only other ingredient of the ration. This mixture not only provided more protein of better quality but also minerals and vitamins (particularly calcium and carotene) necessary to supplement corn. Prior to this, a ration of corn and tankage was considered to be one of the best. It was also believed that tankage adequately supplemented corn in both quantity and quality of protein. In a modern study to investigate further these latter two feeds, Henson *et al.* (1952) made up a basal diet for pigs of corn, tankage, salt, vitamin A and D oil, the vitamins, riboflavin, calcium pantothenate, niacin, and B₁₂, and the antibiotic, terramycin. Supplementing this ration with tryptophan greatly increased the average daily gain and reduced the pounds of feed per 100 pounds of gain. Thus tryptophan appears to be the limiting amino acid in this corn-tankage ration. Beeson *et al.* (1949) demonstrated the minimum level of tryptophan for pigs weighing from 50 to 100 pounds to be 0.4 per cent of DL-tryptophan.

In experiments with rats, Sure (1948) found that the addition of 3 to 5 per cent yeast supplemented a white corn meal diet with the necessary lysine and tryptophan, as well as possibly providing one or more other dietary essentials that stimulated growth. In a corn-soybean oil meal diet, Blight and Powick (1951) did not find that the addition of methionine or lysine had any measurable effect on the growth rate of rats.

According to Hamilton (1950) lysine is the amino acid which severely limits the protein of cottonseed meal. Dyer *et al.* (1949) had shown that 0.2 per cent methionine supplemented a corn-soybean oil meal ration for pigs. With these considerations in mind, Dyer *et al.* (1952) investigated the value of lysine, methionine, and fish solubles in a corn-cottonseed meal diet. They estimated that this basal ration contained about 0.36 per cent methionine or about half of the requirement for pigs. This ration fortified with minerals, vitamins A, D, riboflavin, niacin, pantothenic acid, choline, and vitamin B₁₂ did not support optimum performance. When 0.5 per cent DL-methionine and 0.2 per cent DL-lysine were added, significantly faster daily gains were made. However, further improvement resulted from the addition of soybean oil meal and penicillin to this ration.

Sure (1948b) found no difference between a cultured yeast, soybean flour, dry nonfat milk solids, and dried buttermilk as protein supplements for rats on a diet containing 75 per cent white corn meal. In a mice diet of corn only, Csáky (1947) found that the replacement of half of the corn by fresh baker's yeast gave satisfactory growth. Nicotinic acid did not improve the diet with or without the yeast. The author ascribed the improvement to the protein of the yeast.

VII. Pellagra and Corn

Pellagra is a debilitating disease that has developed in relatively modern history. In fact, its spread throughout the world was coincident with the spread and use of corn meal as a large part of the diet of poor people—occurring since corn was discovered in the Western Hemisphere. Pellagra cases among populations largely consuming other cereals are rare indeed.

This condition was first thought to be brought on by a toxin in corn, but this theory, although perhaps not entirely disproved, has largely

TABLE II
THE MINERAL COMPOSITION OF CORN (85% DRY MATTER)

	<i>Beeson's^a data</i>	<i>National Research^b Council Report No. 2</i>		<i>Kansas^c data</i>
		1946	1947	
Calcium, %	0.0128	0.0194	0.0239	0.008
Phosphorus, %	0.3655	0.2730	0.2620	0.272
Potassium, %	0.3400	0.2850	0.2820	0.298
Iron, %	0.0031	0.00226	0.00185	0.003
Magnesium, %	0.1360	0.1020	0.1109	0.085
Sodium, %	0.0408	0.0100	0.00939	0.003
Chlorine, %	0.0240	0.0410	0.0450	0.043
Sulfur, %	0.1190	—	—	—
Manganese, mg./lb.	5.00	2.43	2.19	3.468
Copper, mg./lb.	3.175	1.820	0.734	1.542
Cobalt, mg./lb.	0.0043	0.0112	0.0081	0.0887
Fluorine, mg./lb.	—	2.3	2.6	—
Iodine, %	—	0.00006	—	—
Zinc, %	0.0017	—	—	—

^a Beeson (1941).

^b Schneider *et al.* (1953a, b).

^c Glendening *et al.* (1952).

given way to a deficiency explanation. For some time it was thought that protein insufficiency was the cause of pellagra. However, this was disproved when it was shown that certain extracts of beef liver or pig thymus completely cured cases. Small amounts of yeast or yeast extract supplying only about 7 g. of protein prevented the disease. A deficiency of one of the water-soluble B vitamins was suspected as being the cause. This specific vitamin was first called the P-P (pellagra-preventing) vitamin.

The black tongue disease in dogs was then found to be identical for this species with pellagra in man. Frost and Elvehjem (1937) and

Elvehjem *et al.* (1937) found that nicotinic acid or nicotinamide cured black tongue.

An acute condition in pigs arising from the same deficiency and involving severe dermatitis, diarrhea, anorexia, and loss of weight could be cured almost miraculously with 60 mg. of nicotinic acid (Chick *et al.*, 1937, 1938). Fouts *et al.* (1937) first cured human pellagra with nicotinic acid.

What is the connection between corn grain and the occurrence of pellagra? One explanation is that corn is deficient in both tryptophan and nicotinic acid (Krehl, 1949). It was found that the addition of the amino acid, tryptophan, to dog diets prevented the symptoms of nicotinic acid deficiency (Hilderberger *et al.*, 1948; Singal *et al.*, 1947–48). Leucke *et al.* (1947) also demonstrated this with pigs. Although our common domestic animals have not been shown to use tryptophan entirely in place of nicotinic acid, large amounts of tryptophan will compensate at least partially for nicotinic acid deficiency. This also explains why adding extra protein to a ration has had a beneficial effect upon pellagra. Thus it is that corn, which is low in the B-complex vitamin, nicotinic acid, and deficient in the amino acid, tryptophan, is thus doubly at fault and conducive to pellagra in man and similar diseases in other species.

VIII. Minerals in Corn

1. The General Mineral Composition of Corn

The mineral content of corn is shown in Table II. It will be noticed that corn is most abundant in phosphorus and potassium. Phosphorus is the most likely to be deficient of these two elements in common livestock rations consisting largely of roughages. It is obvious that we do not depend upon corn grain as a source of minerals. Meyer *et al.* (1950) made a survey of the sodium, potassium, and chlorine content of the more common feeding stuffs. The values of corn and the most common corn by-products are shown in Table III. However, corn constitutes a

TABLE III
SODIUM, POTASSIUM, AND CHLORINE CONTENT OF FEEDS

<i>Feeding stuff</i>	<i>No. samples</i>	<i>Sodium, %</i>	<i>Potassium, %</i>	<i>Chlorine, %</i>
Corn, dent, Grade No. 2	7	0.004 (0.001–0.009)	0.34 (0.27–0.45)	0.06 (0.05–0.07)
Corn gluten feed	5	0.21 (0.02–0.52)	1.06 (0.72–1.44)	0.37 (0.16–0.64)
Corn gluten meal	5	0.04 (0.02–0.05)	0.53 (0.37–0.81)	0.12 (0.08–0.15)

high percentage of many livestock rations and hence does contribute at times an important proportion of the total minerals received by animals.

2. Sodium and Calcium Deficiency

Corn is significant in connection with the pioneering research of Hart *et al.* (1911, 1917) on the physiological effect on growth and reproduction of rations from restricted sources. Their rations consisted entirely of the corn plant, the wheat plant, the oat plant, and a mixture of the three. The ration from the corn plant was the most successful. This consisted of corn stover, corn meal, and corn gluten feed. In the first of the two publications by these authors on this subject, they conclude as follows:

“Those receiving their nutrients from the corn plant were strong and vigorous, in splendid condition all the time and produced young of great weight and vigor.”

However, the heifers that had received wheat straw, ground wheat, and wheat gluten did not perform normally in either growth or reproduction. When oat straw and oat meal were fed, the response of the animals was intermediate between that of corn and of wheat. Where a mixture of all of these plant materials was used, the response of the heifers was less satisfactory than with the corn or oat ration alone but more vigorous than with the wheat rations.

On the wheat rations the heifers failed to show estrus and could not be bred. Marked pathological conditions resulted, such as blindness, feeble and emaciated condition, and abnormal excitability followed by collapse. Those that became pregnant produced weak or dead calves.

The authors attributed the cause for this nutritive failure to two factors in the ration, (1) a poor salt mixture and (2) inherent toxicity in the grain. Although the real causes of this situation were never proved experimentally, we can conclude in the light of more recent knowledge that the first of their conclusions, that there were mineral deficiencies in all but the corn plant rations, is true. Probably it was a calcium deficiency. However, in place of the toxicity factor we now know that a deficiency of vitamin A was the primary cause of the failure of the wheat and oats rations, whereas an adequate amount of the same vitamin was responsible for the success of the corn ration.

Another early experiment concerning corn and minerals is one by Henry (1890) in which he fed corn with and without mineral supplements. The addition of bone meal or wood ashes to the corn ration saved approximately 130 pounds or 28 per cent of corn per 100 pounds of body gain. The feeding of bone meal with corn doubled the strength of the thigh bone, and wood ashes nearly doubled it. There was 50 per

cent more ash in the bones of pigs receiving these minerals than in the others. Since then there have been many feeding trials with pigs fed only corn or combinations of corn with minerals or tankage (or another protein supplement), or both (see Tables IV and V). These strictly corn rations, of course, are progressively improved as their deficiencies in protein, in minerals, and in vitamins are corrected.

On the basis of chemical analysis, McCollum *et al.* (1917) concluded that seeds generally are deficient in sodium, calcium, and chlorine. In a second publication McCollum and Simmonds (1917) tried to evaluate the mineral deficiencies of a mixture of corn and beans. Rather discordant and unexpected results were obtained in feeding experiments with rats, although the authors concluded that sodium and calcium are limiting elements in the mineral content of seeds. The common use of salt leaves only calcium as a dangerously low element in practice. With this background Mitchell and Carman (1926) planned a paired-feeding experiment with rats receiving 87 per cent corn, 10 per cent casein, 2 per cent cod-liver oil, and 1 per cent calcium carbonate. This diet was compared with a second one in which 1 per cent sodium chloride was substituted for an equal amount of corn. Without exception the rats receiving the added sodium chloride made more rapid gains in weight than those receiving no added salt. With all pairs of rats the amount of feed required to produce a gram gain in weight was less for the salt-fed rats than for the controls. Also in balance periods with rats and chickens the rations containing salt gave distinctly more favorable balances of sodium and chlorine than their pair mates on rations low in these elements. The rats without added salt showed a decidedly negative sodium balance, whereas those receiving salt were in approximate sodium equilibrium. Even the rats without salt were in approximate chlorine equilibrium, whereas those receiving salt showed an appreciable positive balance, with the exception of two rats. Equally favorable results were obtained with the chickens. Further, the animals receiving salt and growing more rapidly showed greater retention of nitrogen.

Thus it appears that although sodium approaches adequacy in corn, both of these elements are deficient.

The authors conclude that, "Probably the concentration of both sodium and chlorine in corn is too low to promote maximum growth in rats and chickens."

3. Other Elements

When a basal ration composed of corn, soybean oil meal, corn gluten meal, alfalfa, salt, and limestone containing 12 to 13 p.p.m. of manganese was supplemented with 40 p.p.m. of manganese, Grummer

et al. (1948) found that these pigs gained more rapidly and required fewer pounds of feed per hundred pounds of gain than those unsupplemented with manganese. Pigs receiving 80 p.p.m. of manganese grew more rapidly than the unsupplemented lots but less rapidly than the pigs receiving 40 p.p.m. Pigs given manganese at 160 p.p.m. did no better than the basal group. The authors were unable to demonstrate a correlation between manganese intake and concentration in the tissues. This experiment was in harmony with the earlier work of Keith *et al.* (1942) in which a stiffness was prevented but not cured in hogs weighing about 150 pounds by feeding 50 to 60 p.p.m. of manganese in the basal diet containing 60 per cent corn.

Noland *et al.* (1951) reviewed a number of experiments which gave conflicting data regarding the necessity of adding trace minerals to swine rations. They report experiments in which yellow corn was the only grain in the rations; these rations were improved by the addition of small amounts of iron, copper, manganese, and cobalt. When the rations were supplemented with these trace elements, the pigs made more rapid gain but the feed efficiency was not improved. Further work by Speer *et al.* (1952) indicated that a corn-soybean oil meal ration with other supplements showed a small but significantly greater gain with the addition of iron, copper, manganese, cobalt, and zinc. The authors concluded from chemical analyses that the improved performance was from the addition of copper, manganese, and/or cobalt. In rations containing approximately 70 per cent corn, Dinusson *et al.* (1953) noted that cobalt supplementation increased significantly the rate of gain in growing-fattening swine. Although earlier nutrition experiments with corn did not show the advantage of feeding these trace minerals as have more recent ones, it must be realized that experimental methods today are more precise than they were only a few years ago. Rations are more complete in all other respects than the one under investigation. Thus, deficiencies that were once minor may have become primary deficiencies now, whereas formerly they were by no means the most severe faults in the rations. Further, the corn rations today may be grown on soils that are becoming more deficient in some of the essential minerals, with the result that present-day experiments reveal advantages of trace mineral feeding that earlier trials did not show.

IX. Vitamins in Corn

1. Vitamin A

The content of vitamins known to be present in corn in significant amounts or of particular importance in corn diets is shown in Table IV.

Yellow corn is the only grain that has a significant amount of vitamin A potency (Fraps, 1931). This vitamin A potency of corn results primarily from the presence of one of the coloring substances, cryptoxanthin, as shown by Kuhn and Grundman (1934). Also, work of Fraps and Kemmerrer (1941) indicates that beta-carotene, neocryptoxanthin, and small amounts of K-carotene and alpha-carotene are present in the total carotene content of corn. The beta-carotene equivalent of yellow corn is approximately 0.64 times the crude carotene (Kemmerrer *et al.*, 1942). One of the best known facts about vitamins in corn is that yellow corn has vitamin A activity, whereas white corn

TABLE IV
THE VITAMIN COMPOSITION OF CORN (85% DRY MATTER)

	<i>Ellis^a & Madsen</i>	<i>National Research^b Council Report No. 2</i>	
		1946	1947
Carotene, mg./lb.	2.20	1.33	1.34
Vitamin A, I.U./lb.	1990	—	—
Thiamine, mg./lb.	2.06	1.72	1.63
Niacin, mg./lb.	6.40	9.75	9.92
Riboflavin, mg./lb.	0.60	0.514	0.570
Pantothenic acid, mg./lb.	3.36	2.44	3.08
Folic acid, mg./lb.	—	0.034	0.047
Alpha-tocopherol (Vitamin E)	11.21	—	—

^a Ellis and Madsen (1943).

^b Schneider *et al.* (1953a, b).

does not. This was first shown in 1920 by Steenbock and Boutwell (1920). Following this discovery, Morrison, Bohstedt, and Steenbock fed pigs on white and yellow corn. This work was reported by Russell and Morrison (1920, 1922). These workers showed that it required 16 per cent more white corn than yellow corn to produce 100 pounds of body gain when corn was balanced with tankage or with skim milk. Pigs receiving yellow corn and tankage made an average daily gain of 1.06 pounds, whereas those receiving white corn and tankage gained only 0.63 pound per day. The former required 447 pounds, and the latter required 554 pounds of feed, per 100 pounds of gain.

Mumford (1922) reported that 9 of 10 pigs died on a white corn tankage ration. Another lot on the same ration plus cod-liver oil grew and fattened normally to 275 pounds in weight. This story has been repeated many times in numerous experiments with swine (Lamb and Evvard, 1923; Livesay and Stillwell, 1928; and others as follow).

Loeffel (1921) found that pigs receiving yellow corn and tankage gained 1.01 pounds per day, whereas those receiving white corn and tankage gained only 0.78 pound per head daily. Snyder (1926) fed rations much more complete than many of the period (containing alfalfa hay, wheat shorts, tankage, minerals, and sometimes oats) and found no significant differences between yellow and white corn.

Longwell and Weakley (1932) produced vitamin A deficiency symptoms in pigs in 77 to 98 days on white corn, buckwheat middlings, and tankage, but not when they fed 2.5 per cent linseed oil meal and ground oats. Martin (1935) compared yellow corn with white corn with

TABLE V
YELLOW CORN VERSUS WHITE CORN FOR SELF-FEEDING PIGS IN DRY LOT^a

Lot	Feeds self-fed ^b	Pigs per lot	Days fed	Average weights, pounds		Average daily gain, pounds	Feed for 100 pounds gain, pounds			
				Initial	Final		Corn	Tank- age	Miner- als	Total
1	Yellow corn, tankage	8	70	83.5	213.1	1.86	334.1	26.0	1.1	361.2
2	White corn, tankage	8	84	82.5	213.4	1.56	366.1	29.2	5.1	400.4
3	Yellow corn	8	84	83.7	142.4	0.70	666.3	None	15.5	681.8
4	White corn	8	84	83	128.0	0.54	670.7	None	20.0	690.7

^a From Martin (1935).

^b The mineral mixture self-fed to all of the lots consisted of ground limestone, 55 pounds; 16 per cent acid phosphate, 25 pounds; and common salt, 20 pounds.

and without tankage as a protein supplement. In both of these cases the yellow corn gave much more rapid gains, although, of course, in the protein-deficient ration the gains were much less than in the ration containing tankage. The differences in this demonstration are so striking that they are presented here to illustrate these as well as the tremendous progress that has been made in swine nutrition (Table V).

In the work of Rice *et al.* (1926), 48 pigs with initial weights of 50 to 70 pounds were fed on white corn and tankage and 28 comparable pigs on yellow corn and tankage. Six of those on white corn developed pathological symptoms, and 2 died before they reached market weight. Other pigs fed only 1 ounce of alfalfa meal per head daily with white corn showed none of the symptoms. They also found that the reproductive powers of sows fed on white corn and tankage were gradually reduced. One sow, fed on white corn, after farrowing two normal litters produced dead litters in the third and fourth gestation periods when

her vitamin A reserves had been exhausted. These authors concluded that alfalfa meal or cod-liver oil renders white corn quite as valuable as yellow corn for growing and fattening pigs or for brood sows.

The work of Grimes *et al.* (1929) illustrated how a green-colored forage containing carotene, such as soybean hay, will supplement white corn. This may be shown best by means of the accompanying Table VI. Although this experiment would have conformed more completely to a modern factorial design if there had been a fourth lot of yellow corn, tankage, and soybean hay, it does demonstrate the effectiveness of white corn when properly supplemented for its carotene deficiency.

TABLE VI
SOYBEAN HAY AS A SUPPLEMENT TO WHITE CORN AND TANKAGE FOR GROWING AND FATTENING HOGS^a

<i>Lots</i>	<i>Feeds</i>	<i>Average daily gains, pounds</i>
1	White corn, 9 parts; tankage, 1 part; self-fed.	1.27
2	Yellow corn, 9 parts; tankage, 1 part; self-fed.	1.47
3	White corn, 9 parts; tankage, 1 part; self-fed. Soybean hay, self-fed.	1.60

^a From Grimes *et al.* (1929).

Hostetler *et al.* (1935) found that adding Menhaden fish meal did not supply the missing vitamin A to a ration of white corn and minerals. The deficiencies were prevented by supplementing the ration with cod-liver oil, yellow corn, alfalfa meal, or by green rye pasture. These authors also fed 5 per cent of dried brewers' yeast with the same basal ration to five rats. After 12 to 16 weeks these rats lost weight, and three of them developed ophthalmia. The eyes of three surviving rats cleared up and growth was resumed when 2 per cent of cod-liver oil was added to the ration after 23 weeks. Yeast added to the ration of another lot of rats did not improve growth. The authors concluded that vitamins D, B, and G were not factors in producing the deficiency symptoms observed.

Morrison *et al.* (1920-1921) in early experiments found that yellow corn was no better than white corn for cattle, sheep, and horses that received plenty of green-colored hay.

The potency of any sample of yellow corn for vitamin A activity is usually estimated by determining the carotene content. The possible fallacy of this method of determination is pointed out by Cabell (1953), who shows that any of the methods of measuring vitamin A potency by means of pigment concentration may be inaccurate. Different corns

vary in their vitamin A activity per unit of pigment. He presents data illustrating the variable ratio between biological activity and carotene concentration in different corn samples. The effect of storage was studied, and it was noted that some samples showed a much greater loss of biological activity than they did of apparent carotene content. If corn is a major source of carotene in a feed mixture, this loss may be a serious one; however, corn loses very little protein and energy value owing to storage, even after several years. Thus he concludes that corn three or four years old may still be quite satisfactory for formulating good feed mixtures. It would merely be necessary to provide vitamin A from other sources. Jones *et al.* (1943) discussed the existing literature pertaining to this problem and concluded that after four years of storage corn might retain from 30 to 50 per cent of the original content. In any event, it should not be concluded that corn contains significant vitamin A potency merely because it is yellow.

Aurand *et al.* (1947) have presented evidence that it is possible to breed corn having a higher content of carotene. The carotene content of corn is inherited and is proportional to the genes for yellow color that are present (Manglesdorf and Fraps, 1931). Kemmerrer *et al.* (1942) did not believe that the genetic composition of corn affected the percentage of the various carotenoids in the crude carotene. Aurand *et al.* (1947) have presented evidence that it is possible to breed corn having a higher content of carotene. It is certainly logical that the various vitamin A precursors in corn should be inherited, but it also seems possible that the most potent sources of vitamin A might be inherited separately from the other pigments. Thus the variety of corn as well as its age may well influence its vitamin A potency. It is likewise conceivable that there could be yellow corn deficient in this vitamin.

Also, in considering the relative values of white and yellow corn meal, it must be realized that in applying scientific knowledge to this problem, there are many difficulties to be taken into account in human diet planning. Although yellow corn meal would be preferred from a nutritional standpoint, Dickins (1945) after a survey of four groups of school children in Mississippi concludes that the shortage of white corn meal and the consequent necessity of consuming only yellow corn meal was a mixed blessing. Apparently many low-income families tend to reduce consumption of other beneficial foods such as vegetables and buttermilk when white corn meal is not available. This appears to be the case with temporary shortages of white corn meal, but possibly continued shortage of white corn meal would lead to replacement of white with yellow meal.

Haylett and Smit (1951) report that yellow corn meal in South

Africa is relegated by public prejudice to the status of a cattle feed, and millers avoid grinding it for human consumption.

2. Thiamine

Some reports in the literature (Conner and Straub, 1941; Ellis and Madsen, 1943; Golberg and Thorp, 1945; and Nordgren and Andrews, 1941) show that there is more thiamine in white corn than in yellow corn. Golberg and Thorp (1945) found that corn grown on soil treated with superphosphate had significantly higher concentrations of this vitamin. Hunt *et al.* (1950a) obtained higher values for thiamine when the soil was limed, but lower values during a dry year or when potash was the only treatment in rotation experiments. Results were different when corn was grown continuously. Burkholder and McVeigh (1940) observed that when the nitrogen supply was varied in nutrient media the thiamine content of corn grown therein was increased. However, the thiamine content varied inversely with the phosphorus included in the nutrient media.

Golberg and Thorp gave the thiamine content of yellow corn as 2.8 mg./kg. in South Africa. In India Ahmad *et al.* (1948) determined 2.13 mg./kg. for maize grown in that country. Sarkar *et al.* (1951) found an average value of 4.9 mg./kg. The latter is a mean of 25 samples obtained in co-operation with the National Research Council corn survey mentioned earlier (Schneider *et al.*, 1953). Schultz *et al.* (1941) assayed the thiamine content of corn samples from widely separated areas, finding an average of 5.34 mg./kg. Sarkar *et al.* (1951) present a table of thiamine values from the literature that vary from 2.33 to 8.0 mg./kg. French *et al.* (1951) determined the thiamine content of yellow sweet corn having only 24.6 per cent dry matter at 1.26 mg./kg.

3. Riboflavin

Sarkar *et al.* (1951) also determined the riboflavin of the same samples of corn supplied by the National Research Council Committee on Feed Composition (Schneider *et al.*, 1953). These workers found the mean value to be 1.02 mg./kg. of riboflavin in corn. They present a table of previously determined values by other workers in which the values vary from 0.77 to 2.29 mg./kg. of corn. Hunt *et al.* (1950a) observed that the addition of lime to the soil increased the riboflavin of corn. French *et al.* (1951) determined the riboflavin content of yellow sweet corn at 1.52 mg./kg.

4. Niacin

The importance of nicotinic acid in relation to corn has already been considered in the discussion on pellagra and corn.

The nicotinic acid content of corn was determined by Sarkar *et al.* (1951), who obtained a mean of 28.08 mg./kg. These workers present a table of values from the literature ranging from a minimum of 7.0 to a maximum of 54.1 mg./kg. of corn. French *et al.* (1951) reported the niacin level of yellow sweet corn having only 24.6 per cent dry matter to be 19.4 mg./kg.

Heathcote *et al.* (1952) estimated the milligrams of nicotinic acid per kilogram of one variety each of flint and sweet corn to be 14.2 and 18.1, respectively. These workers also dissected corn kernels into their various anatomical regions, pericarp, aleurone layer, embryo, scutellum, and three or four subdivisions of the endosperm. In the two types

TABLE VII
DISTRIBUTION OF NICOTINIC ACID IN CORN^a

	<i>Flint corn</i> <i>var. Sibthorpe</i>		<i>Sweet corn</i> <i>var. Wisconsin 804C</i>	
	% of <i>grain</i>	% of <i>total</i> <i>niacin</i>	% of <i>grain</i>	% of <i>total</i> <i>niacin</i>
Pericarp	6.5	2.3	5.1	3.2
Aleurone layer	2.2	62.7	3.3	59.2
Endosperm 1	3.9	7.7	5.4	14.0
Endosperm 2	3.9	2.9	5.4	3.6
Endosperm 3	54.2	7.8	65.6	8.0
Endosperm 4	17.6	1.8	—	—
Embryo	1.1	1.7	2.0	2.3
Scutellum	10.6	13.1	13.2	9.7

^a From Heathcote *et al.* (1952).

of corn, 62.7 per cent and 59.2 per cent, respectively, of nicotinic acid were in the aleurone layers. These results are shown in Table VII. The distribution of nicotinic acid is quite different in corn from that of thiamine. The authors call attention to the fact that the scutellum contained about 80 per cent of the thiamine of corn, whereas it has only 10 to 13 per cent of the nicotinic acid. The embryo in both corns contains only about 2 per cent. The authors call attention to the fact that part of the nicotinic acid is present in bound form believed to contain a protein component. This bound form may not be biologically available to some species, but it is believed that this complex is generally hydrolyzed in alkaline medium during digestion, thus liberating the nicotinic acid.

There is little difference in the average niacin content of different

corn hybrids from year to year, but there is considerable difference in the content of this vitamin of each variety of hybrid corn from one location to another. This, concludes Hunt *et al.* (1950b), shows that niacin can be influenced by soil and other environmental factors. An analysis of variance shows that location, hybrid varieties, and interaction of location or hybrid variety with year all show highly significant differences. The differences between years and the interaction of location with hybrid variety were significant, but less than the other sources of variance. The authors were able to select varieties that were very high and very low in niacin content and identify certain areas which tend to produce corn having high or low niacin content. The most extreme values obtained were 17.0 and 30.1 mg./kg., expressed on a moisture-free basis.

In another article these authors (Hunt *et al.*, 1950c) noted that the dry matter and niacin content of stalks and leaves remained remarkably constant until sweet corn ears were well filled with grain. The niacin was highest in the tassels at the time of pollination and then decreased steadily. The niacin content of the pollen was higher than that of the tassel at bloom stage. The highest concentration of niacin in the grain occurred 18 to 20 days after the tassel bloomed. This is the "roasting ear stage" when sweet corn is usually eaten.

Burkholder *et al.* (1944), contrary to the findings of Hunt *et al.* (1950a), believed that "locality" had no influence on the nicotinic acid content of corn. They thought that it was controlled largely by genetic factors, and they demonstrated that the nicotinic acid content of sweet corn was higher than that of common dent corn. This was also demonstrated by the work of Barton-Wright (1944) and Mather and Barton-Wright (1946). Following this lead, Gorfinkel (1948) reasoned that pellagra could be prevented in a human population consuming large quantities of corn by breeding varieties having larger amounts of nicotinic acid. He demonstrated that dent corn of 92 different lines varied in nicotinic acid content from 14.9 to 31.2 mg./kg. His original hypothesis was supported by his experimental work by the following observations: When parental strains had extreme amounts of the vitamin, the offspring had intermediate amounts. Hybrids high in the vitamin came from parents that were also high in it. Further, the fact that there is greater disparity in the nicotinic acid content of different inbred lines than among hybrids also supports the postulate that nicotinic acid content has a genetic basis. The differences in niacin content of single-cross hybrid and inbred lines, all grown in approximately the same environmental conditions, led Ditzler *et al.* (1948) to conclude that it is definitely inherited. This viewpoint has also been furthered by

the work of Richey and Dawson (1948, 1951), Cameron and Leas (1948), and Leng *et al.* (1950).

Gorfinkel *et al.* (1948) concluded that sweet corn, which is relatively high in nicotinic acid, could not be used to increase the content of this vitamin in dent corn. This later conclusion appears to be in harmony with that of Heathcote *et al.* (1952) that nicotinic acid formation in corn grain is an integral part of the carbohydrate metabolism of the endosperm, and hence this vitamin and the different carbohydrates would not be inherited separately.

Except for possible synthesis in the gastrointestinal tract, animals must depend upon food sources of nicotinic acid to supply their needs for vital functions. Singal *et al.* (1948) point out that a decrease in this vitamin in the body of the animal is incompatible with life, particularly when it affects the vital organs, the heart, lungs, spleen, kidney, and blood. In self-protection the animal conserves the nicotinic acid supply in these organs while permitting it to become depleted in muscles and liver. Under such circumstances the laboratory rat reduces his food intake so as to decrease nutritional stress. When this is prevented by forced feeding, acute vitamin deficiency develops rapidly. In diets containing 40 per cent corn grits, the authors demonstrated these physiological changes in the nicotinic acid content of the various organs. Supplementary nicotinic acid or tryptophan prevented the depletion of these body stores of nicotinic acid. The authors interpret their data to mean that tryptophan makes biosynthesis of nicotinic acid possible.

Laguna and Carpenter (1951) noted that the growth depression of rats fed a high-corn diet in the absence of niacin was reduced by steeping the corn in lime water, then neutralizing and drying it. This is a process similar to the one commonly used by generations of Mexican peasants in making "tortillas." When these workers reconstituted corn from starch, germ, corn feed meal, corn gluten, and tricalcium phosphate, the lime water treatment seemed to be effective when applied only to the nonstarchy fractions, the gluten, feed meal, and germ.

Haylett and Smit (1951) noted the tendency in other parts of the world to fortify various cereals. They suggest enriching maize meal with calcium carbonate, milk powder, yeast, fish meal, or soybean meal.

Paul *et al.* (1948) studied the changes in acceptability caused by the addition of varying amounts of dry primary yeast to corn meal. Yellow and white corn meal with 0, 1, 2, and 3 per cent of added yeast were tested. In corn meal mush, corn dodgers, and corn bread the palatability of the yellow corn meal products decreased as the concentration of yeast increased. This trend was also exhibited in the white corn meal products but was not so clearly defined. It was concluded that 1 per

cent of yeast could be added to corn meal without pronounced change in acceptability, but that more than that could be detected. Cederquist (1948) reported great increase in body weight with the addition of 5 per cent cultured yeast to rat diets; however, these authors accept their findings with reservations, since such a diet would be very unpalatable to human subjects. They conclude that the flavor of the yeast would have to be masked under other seasonings and feel that the degree of improvement from such yeast addition has been overestimated.

5. Pantothenic Acid

The pantothenic acid content of corn has been investigated by some of the same authors who studied the concentration of other B-complex vitamins in corn. Sarkar *et al.* (1951) found 6.42 mg./km. of pantothenic acid per kilogram of corn. They compiled a table of values from the literature which varied from a minimum of 1.9 to a maximum of 11.6 mg./km.

Ditzler *et al.* (1948) noted a genetic effect with hybrids grown under similar environmental conditions, but also found that environmental factors played a considerable part in variations in this vitamin. In three papers on the subject, Hunt *et al.* (1950a, b, c) concluded that the pantothenic acid content of hybrids was due less to heredity and more to seasonal differences. They also found that this vitamin was higher in moldy corn than in normal corn and failed to find any effects from fertilization of the soil, although hybrids grown in Ohio seemed to contain more than those grown elsewhere.

X. Correlations of Corn Nutrients

Several workers have tried to discover if there are correlations between the various nutrients of corn. In so far as this would be successful between the various nutrients, values that are difficult to determine could possibly be predicted from the content of the more easily determined nutrients. This might eliminate the need of some of the most difficult and time-consuming chemical determinations and be of great importance in nutrition as well.

Of the 434 correlation coefficients computed by the National Research Council Committee on Feed Composition (Schneider *et al.*, 1953a) only 34 equalled or exceeded 0.5. This does not indicate that correlations between nutrients are very useful. Determination of the content of some nutrients would not help in assessing others. The negative correlations between nitrogen-free extract and protein, fat, and ash are to be expected because nitrogen-free extract is determined by difference. These correlations are shown in Table VIII.

TABLE VIII

SIMPLE CORRELATION COEFFICIENTS BETWEEN NUTRIENTS WHICH AVERAGED OR EXCEEDED 0.30 FOR THE TWO YEARS, 1946 AND 1947^a
(Statistical significance indicated in parentheses)^b

	<i>N-free extract</i>	<i>K</i>	<i>Mg</i>	<i>Cl</i>	<i>Fe</i>	<i>F</i>	<i>Carotene</i>	<i>Thiamine</i>	<i>Calories</i>
Protein	-0.88 (S)	0.33 (s)	0.38 (s)						
Fat	-0.46 (S)								
Ash	-0.32 (S)								
Ca				0.36 (O)					
P			0.34 (s)						
K	-0.30 (s)								
Mg	-0.38 (s)								
Na		-0.33 (O)				0.80 (s)	0.42 (s)		
Cl							0.36 (O)		
Mn	-0.30 (S)				0.32 (s)	0.60 (s)	0.43 (s)		
Cu									
Co	-0.56 (s)					0.39 (s)			
F	-0.41 (O)		-0.61 (s)	0.35 (O)	0.36 (s)	0.52 (O)			-0.41 (O)
Thiamine					0.42 (s)		0.75 (s)		
Niacin							0.60 (s)		0.50 (s)
					-0.30 (s)	-0.32 (O)	0.42 (s)	0.38 (s)	0.51 (s)
Riboflavin									
Pantothenic acid		0.37 (s)		0.47 (O)	0.37 (s)	0.30 (s)	-0.42 (s)		-0.48 (s)

^a Schneider *et al.* (1953a).
^b S = Significant correlation in both years.
s = Significant correlation in one year.
O = Not significant in either year.

The fat of corn was the only nutrient which appeared to have a substantial correlation with the Great Soil Groups classification. There was only a very slight relationship between the mineral content of corn and soil classes.

Hopkins *et al.* (1903) found a correlation between protein and carbohydrates in corn of -0.90 , while the correlation between protein and oil contents was very low.

Significant correlations were found between total ash and iron ($r = 0.517$) and manganese contents ($r = 0.401$) by Duncan *et al.* (1951). Sarkar *et al.* (1951) did not find a significant correlation between the ether extract and thiamine contents of the corn samples investigated, although a positive correlation had been observed by Pulkki and Puutula (1947). Likewise, Sarkar *et al.* (1951) found no correlation between the ether extract or protein contents and riboflavin content of the samples analyzed. Cameron and Teas (1948) observed an inverse relationship between the niacin and starch contents of corn. A significant negative correlation was found between the niacin and protein contents of the corn analyzed by Sarkar *et al.* (1951), but there was no correlation found between the niacin and ether extract contents. Rodriguez *et al.* (1950) also noted a negative correlation between the niacin and protein contents. Gorfinkel (1948) and Sarkar *et al.* (1951) were unable to find any relationship between the protein or ether extract and pantothenic acid contents.

Rodriguez *et al.* (1950) noted, however, that correlations for niacin and pantothenic acid (positive) approached the 5 per cent level of significance, thus indicating there may be some relationship between these components. Earle *et al.* (1946) found in their data high correlation between the amount of oil in the grain and the amount of the germ.

It can be concluded that, although none of these relationships has been found to be particularly useful, these correlations do look hopeful. Perhaps someone may be able to utilize them in nutrition research or practice or in developing corns more valuable for food.

XI. The Effect of Disease on Corn's Nutritive Value

Mitchell and Beadles (1940) found that corn infected with two types of ear rot *Diplodia zeae* Schw. Lev. or *Fusarium moniliforme* (Sheldon) had lowered protein digestibility. Both energy and protein values were impaired for growth. There was marked loss of ether extract.

Mitchell *et al.* (1947) found that the digestibility of the protein from corn infected with the fungus *Nigrospora oryzae* was lower than that of the uninfected corn. Corn infected to the extent of 53 per cent

with this fungus was 84 per cent as heavy as sound corn of the same variety grown under the same conditions. The chemical composition was very similar. It is significant, too, that the digestible protein was utilized better in metabolism, possibly because more of the protein of the damaged corn came from the germ. Corn germ protein is of higher quality than that of the rest of the kernel. Digestibility of the sound corn protein was 81.7 and of the unsound corn, 78.2. However, the rats grew about equally on sound or unsound corn. Since these two opposite effects of digestibility and utilization after absorption tend to neutralize each other, protein from damaged and undamaged corn has about equal value.

Bottomley *et al.* (1950) studied the influence of various temperatures, humidities, and oxygen concentrations on mold growth and biochemical changes in stored yellow corn. Different species of mold were observed with a relative humidity of 80 per cent and over, depending upon the temperatures as follows: *Penicillium* sp. at 25°C., *Aspergillus flavus* at 30°C., *A. glaucus* at 35°C., and *Mucor* sp. at 45°C. Under the conditions of extremely low oxygen tension, these authors did not find a high correlation between mold count and fat acidity ($r = 0.20$). Although this correlation was significant, of chief interest in this study was the variation in total nitrogen content of stored corn thought to be due to the removal of carbohydrates through seed and mold metabolism. It was noted that the nitrogen loss for the different humidities paralleled the losses in dry matter. These were greater as the humidity was increased.

When 4 per cent corn smut was added to the diet of laying hens for a period of three months, no adverse results were noted by Horvath (1930). The smut did not affect their blood composition or their egg-laying capacity.

XII. Parts of Corn

The work of Heathcote *et al.* (1952) in studying nicotinic acid content of dissected parts of the corn kernel has already been discussed. Early publications reporting the chemical composition of different parts of the corn kernel are those of Hopkins (1898, 1899). He also reviewed some much earlier attempts to analyze corn. Hopkins *et al.* (1903) emphasized the importance of breeding corn for special purposes, presented a method for selecting high-protein seed corn (by selecting corn with kernels having a large proportion of horny parts), and presented the data on the proportion and composition of different parts of corn shown in Table IX. Almost a half century later, Earle *et al.* (1946), using methods similar to those of Hopkins *et al.* (1903), obtained comparable values on chemical composition as shown in Table X.

TABLE IX
PERCENTAGE OF DIFFERENT PARTS AND PERCENTAGE COMPOSITION OF EACH PART^a

Names of parts	Per cent of whole	Composition of parts			
		Protein, %	Oil, %	Ash, %	Carbo- hydrates, %
Ear No. 1 (low in protein)					
Tip caps	1.20	7.36	1.16	0.91	90.57
Hulls	5.47	4.97	0.92	0.82	93.29
Horny gluten	7.75	19.21	4.00	0.92	75.87
Horny starch	29.58	8.12	0.16	0.18	91.54
Crown starch	16.94	7.22	0.19	0.32	92.27
Tip starch	10.93	6.10	0.29	0.29	93.31
Germs	9.59	19.91	36.54	10.48	33.07
Mixed waste	18.53	9.90	1.06	0.61	88.43
Whole corn		9.28	4.20	1.41	85.11
Ear No. 3 (high in protein)					
Tip caps	1.62	4.64	1.99	1.87	91.50
Hulls	6.09	3.84	0.76	1.10	94.30
Horny gluten	9.86	24.58	4.61	1.74	69.07
Horny starch	33.79	10.99	0.22	0.21	88.58
Crown starch	10.45	8.61	0.52	0.37	90.50
Tip starch	6.23	7.29	1.36	0.60	90.75
Germs	11.93	19.56	33.71	10.00	36.73
Mixed waste	20.03	12.53	1.15	0.61	85.71
Whole corn		12.85	5.36	1.67	80.12

^a From Hopkins *et al.* (1903).

TABLE X
COMPOSITION OF CORN FRACTIONS^a

Portion of kernel	Proportion of whole grain, %	Ash, %	Crude protein, %	Oil, %	Sugar, %	Starch, %
Endosperm	81.9	0.31	9.4	0.8	0.64	86.4
Germ	11.9	10.10	18.8	34.5	10.81	8.2
Bran	5.3	0.84	3.7	1.0	0.34	7.3
Tip cap	0.8	1.59	9.1	3.8	1.61	5.3

^a From Earle *et al.* (1946).

From Tables IX and X, it will be noted that most of the fat in corn is in the germ, although not all. A study of the fat proportions of corn was made by Baldwin and Sniegowski (1951) which shows that germ oil is primarily a mixture of triglycerides. The fats associated with gluten and fiber contain large amounts of free fatty acids, and that in the starch is predominately free fatty acid. Germ fats were the most unsaturated, contained the least free fatty acids, and had the least unsaponifiable matter. Starch fats were 17 and 90 per cent free fatty acids and contained large amounts of palmitic acid. The gluten and fiber fats contained up to 32 per cent unsaponifiables, and about 20 per cent free fatty acids.

Hominy feed containing 5 per cent fat was found by Vestal and Shrewsbury (1944) to produce some soft pork carcasses. Terrill *et al.* (1951) did not find any difference between corn containing 4.7 per cent and 6.4 per cent fat in the firmness of the carcass or the iodine number of the fat.

XIII. Grinding Corn

1. Corn Meal

Corn grain that is ground without removing the germs or any part of the kernel is called merely *ground corn*, *corn chop*, or *corn meal*, but the latter term may also mean the degermed meal. Corn in which the kernels are broken into several pieces is called *cracked corn*. It takes more power to grind corn fine, and it is not so good for feeding most livestock as that ground more coarsely. However, it is better if corn is ground somewhat finer than cracked corn. With cattle, particularly, cracked corn will pass through the alimentary tract undigested, much as whole corn kernels will.

In large commercial mills, cracked corn or coarsely ground corn is passed over screens to remove any fine pieces. These products are then designated as *screened cracked corn* or *screened ground corn*. They are used for poultry feeds. The fine pieces that were screened out are called *corn feed meal*. This product is slightly higher in crude fiber, in protein, and in fat than ground corn, but averages out to have about the same total feeding value.

The effect of grinding corn was investigated by Garrigus and Mitchell (1935). The net effect of grinding for pigs weighing from 135 to 196 pounds was to increase the value of corn as a source of energy by 3.5 per cent. Its protein value was not greatly changed, although the digestibility of the protein was increased by 13 per cent, because there were greater losses of nitrogen during metabolism with the ground corn.

In an attempt to distinguish between screened or sifted corn meal,

from which the bran had been removed, and the unsifted meal, Naude *et al.* (1950) studied the crude fiber content. They concluded that these two types of corn meal can be distinguished by their crude fiber content. The unsifted had the same fiber content, 2 per cent, as the original grain. Sifted corn meal had a fiber content of about 1 per cent.

Corn is frequently ground in order to mix and feed it more conveniently; however, in the practical feeding of livestock on farms where the corn is grown, the only species of livestock with which grinding pays is mature cattle. Even so, with fattening beef cattle it has been found profitable to feed unground corn when pigs are available to salvage the undigested kernels.

2. *Corn-and-cob Meal*

When whole ears of corn are ground, the resulting product is called *corn-and-cob meal*, *corn ear chops*, or *ground ear corn*. This takes somewhat more power than grinding shelled corn, but one of two processes is saved, i.e., it is not necessary first to shell the corn and then grind it. This bulky feed is excellent for cattle. Normally, this feed consists of about 20 per cent cobs and 80 per cent grain. These cobs or additional cobs, when not in too large amounts, supply somewhat more total digestible nutrients than would be considered possible from their appearance. They contribute practically no digestible protein to the ration. This feed is excellent for farm use. However, it is not of significant value in the commercial feed trade because its increased bulk makes it uneconomical to handle, particularly shipping any great distance. Many experiments in the Corn Belt during the past 50 years have demonstrated the value of corn cobs as feed when properly balanced with protein, minerals, and vitamins.

Although corn-and-cob meal has been prepared and fed to livestock for many years (Allison, 1917; Gerlaugh and Rogers, 1935; Mumford, 1905; Peters, 1933; Vaughn, 1927), the work of Burroughs *et al.* (1945, 1946) and of Beeson (1951; Beeson and Perry, 1952) has brought the value of this feed to our attention more vividly. A new concept is being developed, based on the hypothesis that it is first necessary to feed the microorganisms in the rumen in order to feed the ruminant—particularly on coarse roughages. In these experiments, corn-and-cob meal or ground cobs have played a very important part. The addition of required amounts of protein, mineral, and vitamins appeared to greatly increase the utilization of ground corn cobs.

When Burroughs *et al.* (1946) examined the rumen contents of steers every 4 hours for 24-hour periods, they noted that only slight differences occurred in the rumen contents when whole shelled corn

was compared with ground shelled corn. However, marked differences existed in the water and fiber contents of the rumen when ground ear corn was fed.

The total digestible nutrient content of corn cobs was determined by Burroughs *et al.* (1945) to be 51.6 per cent. From this the authors conclude that, for cattle, cobs are 64 per cent as valuable as the grain itself for energy or fattening purposes. This estimate compares favorably with feed lot experiments which show that the corn cob replacement value of corn grain is approximately 62 per cent. Burroughs *et al.* (1950a) found that corn cob digestion was improved with a supplement of a water extract of dehydrated alfalfa meal or the ash of alfalfa meal. This is interpreted to mean that the inorganic elements in alfalfa are required by the rumen microorganisms and stimulate their activity in digestion.

Burroughs and Gerlough (1949) found that soybean oil meal increased the digestibility of dry matter of rations either with or without corn cobs. Burroughs and co-workers later noted (1949b) that corn cobs could be well utilized even with a very low-protein ration, if starch was not added. Starch decreased the digestibility of fiber (1949a), and it was necessary to increase the level of protein to maintain the same level of roughage digestion. Casein increased the digestibility of a low-protein ground corn cob ration (Burroughs *et al.*, 1950b).

Beeson and Perry (1952) applied these principles and measured the results of their experiments in terms of growth with calves and yearling steers fed soybean oil meal, molasses feed, minerals, and vitamin A and D concentrates in addition to corn cobs. When urea replaced $\frac{1}{3}$ to $\frac{2}{3}$ of the protein equivalent of the soybean oil meal, there was no significant difference in growth rate. When 2 pounds of alfalfa meal was substituted for an equal amount of corn cobs, there was a significant increase in growth.

Swift (1951) determined the digestibility of fiber with sheep fed a ration containing about 40 per cent ground corn cobs. The apparent digestibility of the crude fiber was significantly increased by the addition of alfalfa ash from 43 per cent to 53.8 per cent.

Corn-and-cob meal has been found to be most satisfactory with beef cattle. However, it has been tried with variable success with other farm animals.

Monroe and Krauss (1946a, b) compared ground ear corn with ground shelled corn in simple concentrate mixtures equalized for protein. They concluded that the ground shelled corn is 98 per cent as satisfactory as the ground ear corn. In their experiments there was a slight financial gain by feeding the ground ear corn.

Kennard and Chamberlin (1944, 1946) found that corn-and-cob meal substituted for corn meal in an all mash laying ration decreased egg production slightly. However, these workers point out that better plumage, less feather picking, and less cannibalism resulted. The authors suggest that corn-and-cob meal might be substituted for oats that have previously been included in such rations to prevent the vices of feather picking and cannibalism.

Corn-and-cob meal should not be expected to be a satisfactory feed for pigs because it is too high in fiber content. This has been shown to be true by the work of Kennedy and Robbins (1909). Also, at the Georgia Coastal Plain Experiment Station (Anonymous, 1948-49) comparisons were made of cracked corn with finely ground whole ear corn, both supplemented with protein. It was found that the pigs fed the cracked corn mixture made 40 per cent faster gains than the pigs fed the ground whole ear corn mixture. The pigs fed the cracked corn mixture required 450 pounds of feed per 100 pounds of gain as compared with 686 pounds for the pigs fed the ground whole ear corn. Three such experiments were conducted with pigs weighing approximately 120 pounds at the beginning of the feeding tests. It was believed that if younger pigs had been used the difference would have been greater, because young pigs could not utilize properly the ground cob and husks that were included in the ground snapped corn mixture.

XIV. Comparison with Other Grains

Corn is a fattening feed par excellence. This high-energy feed, that is lower in fiber, adds much to rations. It is the "standard" with which to compare all other grains. Corn, for instance, is the basis of the high-energy poultry rations that are recognized throughout the United States wherever "broilers" are fattened (Scott *et al.*, 1947).

Barley tends to produce bloat in ruminants when fed as the only grain, particularly with alfalfa hay. Corn is frequently fed as the only grain to fattening cattle or lambs. Barley contains over 5 per cent and oats about 11 per cent fiber, whereas corn has only about 2 per cent fiber. Wheat averages somewhat higher than corn in fiber. All of the other grains contain proteins of higher quality (for monogastric animals) as well as averaging somewhat more protein than corn. However none of the grains have truly high-quality protein. Corn contains less mineral matter (calcium, phosphorus, potassium) than the other common grains. Wheat gives slower gains with all species of farm livestock but hogs. However, with all fattening animals except lambs and poultry, equal or less weight of wheat is required per 100 pounds of body

gain than with corn. Corn is worth about 20 per cent more than wheat for fattening lambs.

XV. The Energy Content of Corn

It has been noted that corn is not superior in either quantity or quality of protein. Neither is it a particularly good source of minerals, although its phosphorus content is not deficient. Further, corn is not fed primarily as a source of any of the vitamins unless it be that yellow corn is included in a feed mixture for its vitamin A potency. However, as it has been shown earlier in this chapter, even yellow corn is not a dependable source of this latter vitamin. Then, why is corn so highly regarded? Primarily because it is superior in net energy content. Feeding experiments too numerous to identify, and decades of practical experience in homes and on farms the world over, identify corn as a very palatable and high-energy grain. This is shown in the important position of corn in the high-energy rations used by poultrymen in producing broilers (Scott *et al.*, 1947). Without doubt, its high yield also adds to its value in terms of nutritive energy per acre, a large factor whenever corn is grown. All animal life tends to eat first to satisfy bodily energy requirements, although life cannot continue for long without adequate protein, minerals, and vitamins.

Corn is low in fiber (Table I) and is highly digestible. The digestion coefficient of the organic matter of corn by sheep is 89, by cattle 84, and by swine 86 (Schneider, 1947) when fed with other feeds and with digestibility determined "by difference." The gross energy content of 160 samples of the 1946 crop of corn in the United States was 3863.96 cal./g. (Schneider *et al.*, 1953b). Thirty-six samples of corn (Table I) used in digestion trials contained 3.81 Cal./g. These averaged 83.5 per cent digested and yielded 3.18 digestible Cal./g.

Although corn is the standard (as far as energy is concerned) to which all other feeds are compared (Peterson, 1932; Morrison, 1948), the author is not confident that corn itself has been adequately evaluated for its energy contribution. It is certain that if any energy value is arbitrarily taken for corn, other feeds can be given their approximate ranking in relation to it. The total digestible nutrient content and the net energy content of corn have both been accepted as being slightly over 80 per cent. It is obvious that this value was determined with sheep, which have more efficient digestive powers for concentrates than have cattle (Cipolloni *et al.*, 1951). In extensive studies of digestibility, the author (Schneider, 1947; Schneider *et al.*, 1950, 1951, 1952) has found only a relatively few digestion trials with cattle that yielded a total digestible nutrient content of 80 per cent or greater for corn with

85 per cent dry matter content. Although it is recognized that the character of the base feed may influence the digestibility of any feed determined "by difference," there is nothing in these corn data to indicate that these were influenced by the kind of hay fed. Some of the lowest total digestible nutrient values of corn were obtained when it was fed with alfalfa hay or when linseed oil meal was fed to balance the ration.

If cattle eat 94 per cent of all feed consumed by ruminants (Jennings, 1946) it is important that the energy utilized from corn, the standard, be determined in carefully performed balance and production

TABLE XI

DIVISION OF THE ENERGY OF CORN (85% DRY MATTER) IN ENERGY METABOLISM
EXPERIMENTS WITH CATTLE^a

<i>Feed</i>	<i>Gross energy</i>	<i>Feces</i>	<i>Digestible energy</i>	<i>Urine</i>	<i>Methane</i>	<i>Metab- olizable energy</i>	<i>Heat incre- ment</i>	<i>Net energy</i>
<i>Corn Meal</i>								
Cal./kg.	3776	453	3323	134	360	2829	1219	1610
Therms/100#	171.3	20.6	150.7	6.1	16.3	128.3	55.3	73.0
Per cent	100	12.0	88.0	3.6	9.5	74.9	32.3	42.6

^a Armsby and Fries (1915).

experiments with cattle. In fact, as over 40 per cent of the annual corn crop is estimated to be fed to swine, exact evaluation for this species should not be overlooked. If the present measures of energy do not accurately assess the energy value of corn, it then evolves upon nutrition workers to improve them or devise new ones. The division of the energy in corn as determined in one experiment with steers by Armsby and Fries (1915) calculated to 85 per cent dry matter is given in Table XI.

Thus, it appears that although corn is one of the largest sources of energy in livestock rations, it has not been adequately evaluated from this aspect of its utilization.

XVI. Corn Products Not Discussed

The nutritive value of the many by-products of corn represents another story that cannot be included in this chapter. These valuable by-products include corn bran, corn grits, corn gluten feed, corn gluten meal, malt processed corn, maltose process corn gluten feed, hominy feed, corn oil meal, corn germ meal, corn screenings, and dried corn syrup. Corn stover is a farm by-product occurring in the production of corn which is sometimes used for feeding livestock and sometimes not.

Also, there are the primary products involving the entire corn plant (1) cut and fed as a green soiling crop, (2) cut and shocked as dry corn fodder, or (3) chopped and ensiled as corn silage.

XVII. Summary and Conclusions

The nutritive value of corn has been discussed from the standpoint of this grain's nutrient composition in terms of protein, minerals, vitamins, and energy. It is concluded that although corn does supply considerable amounts of all of these dietary essentials because it is fed in such large amounts, its greatest contribution is that it is an excellent source of nutritive energy.

REFERENCES

- AHMAD, B., MEHRA, S. L., and BHARIHOKE, G. 1948. Thiamin content of common Punjab foodstuffs in the raw and cooked state. *Ann. Biochem. and Exptl. Med. (India)* **8**: 89-92.
- ALLISON, H. O. 1917. Preparation of corn for fattening two-year-old steers. *Missouri Agr. Expt. Sta. Bull.* **149**.
- ANONYMOUS. 1924. Soft corn—how to store and feed it. *Illinois Agr. Expt. Sta. Circ.* **293**.
- ANONYMOUS. 1945. Save immature corn by ensiling. *Agr. Eng. Plans Sheet No.* **9**.
- ANONYMOUS. 1947. When you have soft corn. *Iowa Agr. Expt. Sta. Pamphlet* **122**.
- ANONYMOUS. 1948-49. Swine investigations. *Georgia Coastal Plain Agr. Expt. Sta. 29th Ann. Rept.*, p. 54.
- ARMSBY, H. P., and FRIES, J. A. 1915. Net energy values of feeding stuffs for cattle. *J. Agr. Research* **3**: 435-491.
- AURAND, L. W., MILLER, R. C., and HUBER, L. L. 1947. The influence of heredity on the carotene content of corn. *Science* **106**: 493-494.
- AURAND, L. W., and MILLER, R. C. 1949. Influence of heredity on the crude protein and carotene contents of corn. *Federation Proc.* **8**: 378.
- AURAND, L. W., MILLER, R. C., and HUBER, L. L. 1950. Influence of heredity on carotene and protein contents of corn. *Pennsylvania Agr. Expt. Sta. Bull.* **526**.
- BALDWIN, A. R., and SNIEGOWSKI, M. S. 1951. Fatty acid compositions of lipids from corn and grain sorghum kernels. *J. Am. Oil Chemists' Soc.* **28**: 24-27.
- BARTON-WRIGHT, E. C. 1944. The microbiological assay of nicotinic acid in cereals and other products. *J. Biol. Chem.* **38**: 314-319.
- BECHTEL, H. E., ATKESON, F. W., FENTON, F. C., and CARLETON, W. M. 1945. Pit silos for the storage of atlas sorgho grain and of soft corn. *J. Animal Sci.* **4**: 438-452.
- BEESON, K. C. 1941. The mineral composition of crops with particular reference to the soils in which they were grown. *U. S. Dept. Agr. Misc. Publ.* **369**.
- BEESON, W. M. *et al.* 1949. Effect of tryptophan deficiency on a pig. *J. Animal Sci.* **8**: 531-540.
- BEESON, W. M., and PERRY, T. W. 1952. Balancing the nutritional deficiencies of roughages for beef steers. *J. Animal Sci.* **11**: 501-515.
- BLIGHT, J. C., and POWICK, W. C. 1951. The value of methionine, lysine and vitamin B₁₂ as supplements to a corn-soybean meal diet for pigs and rats. *J. Animal Sci.* **10**: 1039.

- BOTTOMLEY, R. A., CHRISTENSEN, C. M., and GEDDES, W. F. 1950. The influence of various temperatures, humidities, and oxygen concentrations on mold growth and bio-chemical changes in stored yellow corn. *Cereal Chem.* **27**: 271-296.
- BURKHOLDER, P. R., and McVEIGH, I. 1940. Studies on thiamin in green plants with the *Phycomyces* assay method. *Am. J. Botany* **27**: 853-861.
- BURKHOLDER, P. R., McVEIGH, I., and MOYER, D. 1944. Niacin in Maize. *Yale J. Biol. and Med.* **16**: 659-663.
- BURROUGHS, W., and GERLAUGH, P. 1949. The influence of soybean oil meal upon roughage digestion in cattle. *J. Animal Sci.* **8**: 1-8.
- BURROUGHS, W., GALL, L. S., GERLAUGH, P., and BETHKE, R. M. 1950b. The influence of casein upon roughage digestion in cattle with rumen bacteriological studies. *J. Animal Sci.* **9**: 214-220.
- BURROUGHS, W., GERLAUGH, P., and BETHKE, R. M. 1950a. The influence of alfalfa hay and fractions of alfalfa hay upon the digestion of corn cobs. *J. Animal Sci.* **9**: 207-213.
- BURROUGHS, W., GERLAUGH, P., EDGINGTON, B. H., and BETHKE, R. M. 1949b. Further observations on the effect of protein upon roughage digestion in cattle. *J. Animal Sci.* **8**: 9-18.
- BURROUGHS, W., GERLAUGH, P., EDGINGTON, B. H., and BETHKE, R. M. 1949c. The influence of corn starch upon roughage digestion in cattle. *J. Animal Sci.* **8**: 271-278.
- BURROUGHS, W., GERLAUGH, P., SCHALK, A. F., SILVER, E. A., and KUNKLE, L. E. 1945. The nutritive value of corn cobs in beef cattle rations. *J. Animal Sci.* **4**: 375-386.
- BURROUGHS, W., GERLAUGH, P., SILVER, E. A., and SCHALK, A. F. 1946. The amounts of feeds and nutrients in the rumen of cattle throughout a 24-hour period as affected by plane of nutrition and character of ration. *J. Animal Sci.* **5**: 338-349.
- CABELL, C. A. 1953. Yellow corn as a source of vitamin A in animal feeds. *Feed Age* **3**, (8): 34-37.
- CAMERON, J. W., and TEAS, H. J. 1948. Relation between nicotinic acid and carbohydrate in a series of maize endosperm genotypes. *Proc. Natl. Acad. Sci. U. S.* **34**: 390-398.
- CARLSON, A. J., and HOELZEL, F. 1949. Influence of texture of food on its acceptance by rats. *Science* **109**: 63-64.
- CEDERQUIST, D. C., BENNETT, B. V., PLUMMER, J. A., and OHLSON, M. A. 1948. Nutritional studies. *J. Am. Dietet. Assoc.* **24**: 676-678.
- CHICK, H., MACRAE, T. E., MARTIN, A. J. P., and MARTIN, C. J. 1937. Curative action of nicotinic acid of pigs suffering from the effects of a diet consisting largely of maize. *Biochem. J.* **32**: 10-12.
- CHICK, H., MACRAE, T. F., MARTIN, A. J. P., and MARTIN, C. J. 1938. Experiments with pigs on a pellagra-producing diet. *Biochem. J.* **32**: 844-854.
- CIPOLLONI, M. A., SCHNEIDER, B. H., LUCAS, H. L., and PAVLECH, H. M. 1951. Significance of the differences in digestibility of feeds by cattle and sheep. *J. Animal Sci.* **10**: 337-343.
- CONNER, R. T., and STRAUB, G. J. 1941. The thiamin and riboflavin contents of wheat and corn. *Cereal Chem.* **18**: 671-677.
- CREVEAUX-BOURGAT, J., TERRIONE, T., and JACQUOT, R. 1949. Nouvelles études sur la valeur alimentaire du Mais: facteur limitant et relations aminoacides-niacine. *Compt. rend.* **229**: 313-315.
- CŠÁKY, T. Z. 1947. Improving the biological value of corn (maize) with fresh baker's yeast. *Kísérletügyi Kozlemenyek* **47-49**: 57-59.

- DAUGHERTY, C. M. 1914. The agricultural outlook, The world corn crop. *U. S. Dept. Agr. Farmers' Bull.* **581**.
- DICKINS, D. 1945. Some effects of a white corn meal shortage. *J. Am. Dietet. Assoc.* **21**: 287-288.
- DINUSON, W. E., KLOSTERMAN, E. W., LASLEY, E. L., and BUCHANAN, M. L. 1953. Cobalt, alfalfa and meal scraps in drylot rations for growing-fattening pigs. *J. Animal Sci.* **12**: 623-627.
- DITZLER, L., HUNT, C. H., and BETHKE, R. M. 1948. Effect of heredity on the niacin and pantothenic acid content of corn. *Cereal Chem.* **25**: 273-279.
- DOBBINS, F. A., KRIDER, J. L., HAMILTON, T. S., and TERRILL, S. W. 1949. Comparison of high and low protein corn for swine. *J. Animal Sci.* **8**: 617.
- DOBBINS, F. A., KRIDER, J. L., HAMILTON, T. S., EARLEY, E. B., and TERRILL, S. W. 1950a. Comparison of high and low protein corn for growing-fattening pigs in drylot. *J. Animal Sci.* **9**: 625-633.
- DOBBINS, F. A., KRIDER, J. L., HAMILTON, T. S., and TERRILL, S. W. 1950b. Comparison of high and low protein corn as evaluated by the biological value method. *J. Animal Sci.* **9**: 654.
- DOTY, D. M., BRUNSON, A. M., JOHNSON, D. L., and BERGDOLL, M. S. 1943. Investigate the chemical composition and nutritive value of corn as related to its genetic constitution. *Indiana Agr. Expt. Sta. 56th Ann. Rept.*, p. 48.
- DYER, I. A., HARRISON, J. T., NICHOLSON, W. S., JR., and CULLISON, A. E. 1952. Penicillin, lysine, methionine and fish solubles supplement a corn-degossypolized cottonseed meal ration for weanling pigs. *J. Animal Sci.* **11**: 465-473.
- DYER, I. A., KRIDER, J. L., and CARROLL, W. E. 1949. Known and unidentified factors supplement a corn-soybean meal ration for weanling pigs in dry-lot. *J. Animal Sci.* **8**: 541-549.
- EARLE, F. R., CURTIS, J. J., and HUBBARD, J. E. 1946. The composition of the component parts of the corn kernel. *Cereal Chem.* **23**: 504-511.
- EGGERT, R. G., BRINEGAR, M. J., and ANDERSON, C. R. 1951. The effect of supplementing normal and high protein corn with lysine and tryptophane for swine. *J. Animal Sci.* **10**: 1047.
- ELLIS, N. R., and MADSEN, L. L. 1943. The vitamin content of animal feedstuffs. *U. S. Dept. Agr., A. H. D., Mimeo. Circ.* **61**.
- ELVEHJEM, C. A., MADDEN, R. J., STRONG, F. M., and WOOLEY, D. W. 1937. Relation of nicotinic acid and nicotinic acid amide to canine black tongue. *J. Am. Chem. Soc.* **59**: 1767-1768.
- FOUTS, P. J., HELMER, O. M., LEPKOVSKY, S., and JUKES, T. H. 1937. Treatment of human pellagra with nicotinic acid. *Proc. Soc. Exptl. Biol. Med.* **37**: 405-407.
- FRAPS, G. S. 1931. Variations in vitamin A and in chemical composition of corn. *Texas Agr. Expt. Sta. Bull.* **422**.
- FRAPS, G. S., and KEMMERRER, A. R. 1941. Determination of carotene and cryptoxanthin in yellow corn. *Ind. Eng. Chem., Anal. Ed.*, **13**: 806-809.
- FRENCH, R. B., ABBOTT, O. D., and TOWNSEND, R. O. 1951. Levels of thiamine, riboflavin and niacin in Florida-produced foods. *Florida Agr. Expt. Sta. Bull.* **482**.
- FREY, K. J. 1949. The inheritance of protein and certain of its components in maize. *Agron. J.* **41**: 113-117.
- FREY, K. J. 1951. The interrelationship of proteins and amino acids in corn. *Cereal Chem.* **28**: 123-132.
- FREY, K. J., BRIMBALL, B., and SPRAGUE, G. F. 1949. The effect of selection upon protein quality in the corn kernel. *Agron. J.* **41**: 399-403.

- FROST, D. V., and ELVEHJEM, C. A. 1937. Further studies on factor W. *J. Biol. Chem.* **121**: 255-273.
- GARRIGUS, W. P., and MITCHELL, H. H. 1935. The effect of grinding on the digestibility of corn by pigs and on its content of metabolizable energy. *J. Agr. Research* **50**: 731-735.
- GERLAUGH, P., and ROGERS, H. W. 1935. Corn-and-cob meal versus shelled corn for yearlings and calves. *Ohio Agr. Expt. Sta. Bimo. Bull.* **173**.
- GERLAUGH, P., and ROGERS, W. H. 1936. Corn cob meal vs. shelled corn for fattening yearlings and calves. *Ohio Agr. Expt. Sta. Bimo. Bull.* **179**: 34.
- GLENDENING, B. L., SCHRENK, W. G., PARRISH, D. B., and SMITH, E. F. 1952. Mineral content of certain feeds used in north central Kansas. *J. Animal Sci.* **11**: 516-523.
- GOLBERG, L., and THORP, J. M. 1945. A survey of vitamins in African foodstuffs. III. The thiamine content of maize, Kaffer, and other cereals. *S. African J. Med. Sci.* **10**: 1-8.
- GORFINKEL, L. 1948. The influence of crossing on the nicotinic acid content of maize. *J. Agr. Sci.* **38**: 339-342.
- GRIMES, J. D., SEWELL, W. E., and TAYLOR, W. C. 1929. Soybean hay as a supplement to white corn and tankage for growing and fattening hogs. *Alabama Agr. Expt. Sta. Ann. Rept.*
- GRUMMER, R. H., BENTLEY, O. G., PHILLIPS, P. H., and BOHSTEDT, G. 1948. The effect of manganese supplementation on the growth of swine fed rations high in corn by-products. *J. Animal Sci.* **7**: 527.
- HAMILTON, T. S. 1950. Proteins and amino acids. *Flour and Feeds* **51**: 10-14.
- HAMILTON, T. S., HAMILTON, B. C., JOHNSON, B. C., and MITCHELL, H. H. 1951. The dependence of the physical and chemical composition of the corn kernel on soil fertility and cropping system. *Cereal Chem.* **28**: 163-176.
- HANSEN, D. W., BRIMHALL, B., and SPRAGUE, G. F. 1946. Relationship of zein to the total protein of corn. *Cereal Chem.* **23**: 329-335.
- HART, E. B., MCCOLLUM, E. V., STEENBOCK, H., and HUMPHREY, G. C. 1911. Physiological effect on growth and reproduction of rations balanced from restricted sources. *Wisconsin Agr. Expt. Sta. Research Bull.* **17**.
- HART, E. B., MCCOLLUM, E. V., STEENBOCK, H., and HUMPHREY, G. C. 1917. Physiological effect on growth and reproduction of rations balanced from restricted sources. *J. Agr. Research* **10**: 175-198.
- HAYLETT, D. G., and SMIT, R. J. 1951. Maize as human food. *Farming in S. Africa* **26**: 217-221.
- HEATHCOTE, J. G., HINTON, J. J. C., and SHAW, B. 1952. The distribution of nicotinic acid in wheat and maize. *Proc. Roy. Soc. (London)* **B139**: 276-287.
- HEIDENREICH, C. J., and WILSON, R. F. 1952. Immature corn for growing-fattening pigs. *J. Animal Sci.* **11**: 763.
- HENRY, W. A. 1890. Feeding bone meal and hard wood ashes to hogs living on corn. *Wisconsin Agr. Expt. Sta. Bull.* **25**.
- HENSON, J. N., BEESON, W. M., and PERRY, T. W. 1952. Vitamin and amino acid supplementation of corn-tankage rations for growing pigs. *J. Animal Sci.* **11**: 764.
- HILDERBERGER, C., GULLBURG, M. E., MORGAN, A. F., and LEPKOSKEY, S. 1948. Concerning the mechanism of the mammalian conversion of tryptophan into kynurenine, kynurenic acid, and nicotinic acid. *J. Biol. Chem.* **175**: 471-472.
- HOGAN, A. G. 1917. Corn as a source of protein and ash for growing animals. *J. Biol. Chem.* **29**: 485-493.
- HOPKINS, C. G. 1898. The chemistry of the corn kernel. *Illinois Agr. Expt. Sta. Bull.* **53**.

- HOPKINS, C. G. 1899. Improvement in the chemical composition of the corn kernel. *Illinois Agr. Expt. Sta. Bull.* **55**.
- HOPKINS, C. G., SMITH, L. H., and EAST, E. M. 1903. The structure of the corn kernel and the composition of its different parts. *Illinois Agr. Expt. Sta. Bull.* **87**.
- HORVATH, A. A. 1930. Studies in blood composition of animals under pathological conditions. III. Feeding hens with corn smut. *Poultry Sci.* **9**: 313-319.
- HOSTETLER, E. H., FOSTER, J. E., and HALVERSON, J. O. 1935. Vitamin A deficiency—a cause of lameness and death among swine. *North Carolina Agr. Expt. Sta. Tech. Bull.* **52**.
- HUNT, C. H., RODRIQUEZ, L. D., and BETHKE, R. M. 1950a. The environmental and agronomical factors influencing the thiamine, riboflavin, niacin, and pantothenic acid content of wheat, corn, and oats. *Cereal Chem.* **27**: 79-96.
- HUNT, C. H., RODRIQUEZ, L. D., and BETHKA, R. M. 1950b. The niacin and pantothenic acid content of certain Ohio corn hybrids. *Cereal Chem.* **27**: 149-156.
- HUNT, C. H., RODRIQUEZ, L. D., and BETHKE, R. M. 1950c. The effect of maturity on the niacin and pantothenic acid content of the stalks and leaves, tassels, and grain of four sweet corn varieties. *Cereal Chem.* **27**: 157-161.
- JENNINGS, R. D. 1946. Feed consumed by livestock, 1941-42, by states. *U. S. Dept. Agr., Bur. Agr. Econ.* p. 40.
- JOHNSON, I. B., JOHNSON, L. E., WRIGHT, T. H., FENN, F. U., and BURKITT, W. H. 1943. Soft corn for fattening livestock. *South Dakota Agr. Expt. Sta. Circ.* **48**.
- JONES, D. B., FRAPS, G. S., THOMAS, B. H., and ZELENY, L. 1943. The effect of storage of grains on their nutritive value. *Natl. Research Council (U. S.), Reprint and Circ. Ser.* **116**.
- KEITH, T. B., MILLER, R. C., THORP, W. T. S., and McCARTY, M. A. 1942. Nutritional deficiencies of a concentrate mixture composed of corn, tankage, soybean oil meal, and alfalfa meal for growing pigs. *J. Animal Sci.* **2**: 120-125.
- KEMMERRER, A. R., FRAPS, G. S., and MANGLESDORF, P. C. 1942. The relation between the vitamin-A-active carotenoids in corn and the number of genes for yellow color. *Cereal Chem.* **19**: 525-528.
- KENNARD, D. C., and CHAMBERLIN, V. D. 1944. Corn-and-cob meal for growth of pullets and egg production. *Ohio Agr. Expt. Sta. Bimo. Bull.* **29**: 268-269.
- KENNARD, D. C., and CHAMBERLIN, V. D. 1946. Corn-and-cob meal vs. ground shelled corn in rations for chickens. *Ohio Agr. Expt. Sta. Bimo. Bull.* **31**: 104-113.
- KENNARD, D. C., and CHAMBERLIN, V. D. 1946. Corn-and-cob meal vs. ground shelled corn in rations for chickens. *Ohio Agr. Expt. Sta. Bimo. Bull.* **241**.
- KENNEDY, W. J., and ROBBINS, E. D. 1909. Preparation of corn for hogs. *Iowa Agr. Expt. Sta. Bull.* **106**.
- KREHL, W. A. 1949. Niacin in amino acid metabolism. *Vitamins and Hormones* **7**: 111.
- KUHN, R., and GRUNDMANN, C. 1934. Krypto-xanthin aus Gelbem Mais (Uber das Vitamin des Wachstums, VI. Mitteil.). *Ber. deut. chem. ges.* **67**: 593-598.
- LAGUNA, J., and CARPENTER, K. J. 1951. Raw vs. processed corn in niacin-deficient diets. *J. Nutrition* **45**: 21-28.
- LAMB, L. A. R., and EVVARD, J. M. 1923. Observations on the vitamin A requirements of swine. *Proc. Am. Soc. Animal Production*, pp. 136-141.
- LENG, E. R., CURTIS, J. J., and SHEKLETON, M. C. 1950. Niacin content of waxy, sugary, and dent F₂ segregating kernels in corn. *Science* **111**: 665-666.
- LEUCKE, R. W., McMILLIN, W. N., THORP, F., JR., and TULL, C. 1947. The relationship of nicotinic acid, tryptophan and protein in the nutrition of the pig. *J. Nutrition* **33**: 251-261.

- LIVESAY, E. A., and TILLWELL, E. C. 1928. Comparative tests of certain feeds in rations for pigs. *West Virginia Agr. Expt. Sta. Bull.* **213**.
- LOEFFEL, W. J. 1921. A comparison of the feeding values of white and yellow corn. *Nebraska Agr. Expt. Sta. Ann. Rept.* 1924.
- LONGWELL, J. H., and WEAKLEY, C. E., JR. 1932. Some observations on pigs receiving vitamin A deficient rations. *Proc. Am. Soc. Animal Production*, pp. 169-173.
- MANGLESORF, P. C., and FRAPS, G. S. 1931. A direct quantitative relationship between vitamin A in corn and the number of genes for yellow pigmentation. *Science* **73**: 241-242.
- MARAIS, J. S. C., and SMUTS, D. B. 1940. The biological value of the proteins of maize and maize supplemented with lysine and tryptophane. *Onderstepoort J. Vet. Sci. Animal Ind.* **15**: 197-204.
- MARTIN, E. 1935. Use of forage crops for growing a fattening swine. *Arkansas Agr. Expt. Sta. Bull.* **321**.
- MATHER, K., and BARTON-WRIGHT, E. C. 1946. Nicotinic acid in sugary and starchy maize. *Nature* **157**: 109-110.
- MCCOLLUM, E. V., SIMMONDS, N., and PITZ, W. 1917a. The supplementary dietary relationship between leaf and seed as contrasted with combinations of seed with seed. *J. Biol. Chem.* **30**: 13-32.
- MCCOLLUM, E. V., and SIMMONDS, N. 1917b. A biological analysis of pellagra-producing diets. I. The dietary properties of mixtures of maize kernel and bean. *J. Biol. Chem.* **32**: 26-61.
- MEYER, J. H., GRUNERT, R. R., GRUMMER, R. H., PHILLIPS, P. H., and BOHSTEDT, G. 1950. Sodium, potassium and chlorine content of feeding stuffs. *J. Animal Sci.* **9**: 153-156.
- MILLER, R. C., AURAND, L. W., and FLACK, W. R. 1950. Amino acids in high and low protein corn. *Science* **112**: 57-58.
- MITCHELL, H. H., and BEADLES, J. R. 1940. The impairment in nutritive value of corn grain damaged by specific fungi. *J. Agr. Research* **61**: 135-142.
- MITCHELL, H. H., and BEADLES, J. R. 1944. Corn germ: a valuable protein food. *Science* **99**: 129-130.
- MITCHELL, H. H., BEADLES, J. R., KOEHLER, B., and DUNGAN, G. H. 1947. Impairment in nutritive value of corn grain damaged by *Nigrospora oryzae*. *J. Animal Sci.* **6**: 352-358.
- MITCHELL, H. H., and CARMAN, G. G. 1926. Does the addition of sodium chloride increase the value of a corn ration for growing animals? *J. Biol. Chem.* **68**: 165-181.
- MITCHELL, H. H., HAMILTON, T. S., and BEADLES, J. R. 1952. The relationship between the protein content of corn and the nutritional value of the protein. *J. Nutrition* **48**: 461-476.
- MONROE, C. F., and KRAUSS, W. E. 1946a. Ground ear corn as compared to ground shelled corn in a simple grain mixture for milk production. *J. Dairy Sci.* **29**: 539-540.
- MONROE, C. F., and KRAUSS, W. E. 1946b. Simple vs. complex grain mixtures in dairy rations. III. The effect of substituting ground ear corn for ground shelled corn in the simple grain mixture. *Ohio Agr. Expt. Sta. Bimo. Bull.* **240**.
- MORRISON, F. B. 1948. "Feeds and Feeding," 21 ed. Appendix Table II. The Morrison Publishing Co., Ithaca, New York.
- MORRISON, F. B., BOHSTEDT, G., and FARGO, J. M. 1920-21. Yellow corn vs. white corn for stock feeding. *Ann. Rept. Wisconsin Agr. Expt. Sta. Bull.* **339**.
- MORRISON, F. B., BOHSTEDT, G., and FARGO, J. M. 1923. Yellow versus white corn for swine feeding. *Wisconsin Agr. Expt. Sta. Bull.* **352**: 18-21.

- MORRISON, F. B., HULCE, R. S., and HUMPHREY, G. C. 1920-21. Yellow vs. white corn for other stock. *Ann. Rept. Wisconsin Agr. Expt. Sta. Bull.* **339**.
- MUMFORD, H. W. 1905. Comparison of methods of preparing corn and clover hay for fattening steers. *Illinois Agr. Expt. Sta. Bull.* **103**.
- MUMFORD, H. W. 1922. *Illinois Agr. Expt. Sta. Ann. Rept.*
- MYBURGH, S. J. 1946. The biological values of the proteins of some South African (whole seed) maize varieties. *J. Vet. Sci.* **21**: 57-77.
- NAUDE, C. P., BRUWER, P. V. D. M., and PRETORIUS, W. P. 1950. The crude fibre content of sifted and unsifted maize meal. *Union S. Africa, Dept. Agr. Bull.* **313**: 12.
- NOLAND, P. R., WILLMAN, J. P., and MORRISON, F. B. 1951. Vitamin and mineral supplements for growing and fattening pigs in drylot. *J. Animal Sci.* **10**: 875-884.
- NORDGREN, R., and ANDREWS, J. S. 1941. The thiamin content of cereal grains. *Cereal Chem.* **18**: 802-811.
- OSBORNE, T. B., and MENDEL, L. B. 1914. Amino acids in nutrition and growth. *J. Biol. Chem.* **17**: 325-349.
- PAUL, P., FRUEH, M., and OHLSON, M. A. 1948. Corn meal and macaroni products containing dry primary yeast. I. Palatability and acceptability. *J. Am. Dietet. Assoc.* **24**: 673-675.
- PETERS, W. H. 1933. Selection and purchase of feeders and rations for fattening beef cattle. *Minnesota Agr. Expt. Sta. Bull.* **300**.
- PETERSON, W. E. 1932. A formula for evaluating feeds on the basis of digestible nutrients. *J. Dairy Sci.* **15**: 293-297.
- PULKKI, L. H., and PUUTULA, K. 1947. Thiamine distribution in wheat, rye, barley and oats. *Cereal Chem.* **24**: 333-345.
- RICE, J. B., MITCHELL, H. H., and LOIBLE, R. J. 1926. A comparison of white and yellow corn for growing and fattening swine and for brood sows. *Illinois Agr. Expt. Sta. Bull.* **281**.
- RICHEY, F. D., and DAWSON, R. F. 1948. A survey of the possibilities and methods of breeding high-niacin corn (maize). *Plant Physiol.* **23**: 238-254.
- RICHEY, F. D., and DAWSON, R. F. 1951. Experiments on the inheritance of niacin in corn (maize). *Plant Physiol.* **26**: 475-493.
- ROBISON, W. L. 1922. *Ann. Rept. Ohio Agr. Expt. Sta. Bull.* **362**.
- ROBISON, W. L. 1939. Hybrid and open-pollinated corns for pigs. *Ohio Agr. Expt. Sta. Bimo. Bull.* **201**: 156-163.
- ROBISON, W. L. 1944. Palatability and feeding value of different corns for pigs. *Ohio Agr. Expt. Sta. Bimo. Bull.* **228**: 188-206.
- RODRIGUEZ, L. D., HUNT, C. H., and BETHKE, R. M. 1950. The protein, niacin, and pantothenic acid contents of corn inbred lines. *Cereal Chem.* **27**: 67-70.
- ROSS, C. V., GARRIGUS, U. S., HAMILTON, T. S., and EARLEY, E. B. 1952. Comparison of high, medium-high, and low-protein corn for fattening lambs. *J. Animal Sci.* **11**: 774.
- ROSS, C. V., TERRILL, S. W., and BECKER, D. E. 1952. Supplementing high- and low-protein corn for growing-fattening pigs. *J. Animal Sci.* **11**: 774.
- RUSK, H. P., and SNAPP, R. R. 1928. The utilization of soft corn in beef cattle feeding. *Illinois Agr. Expt. Sta. Bull.* **313**.
- RUSSELL, H. L., and MORRISON, F. B. 1920. New farm facts. *Wisconsin Agr. Expt. Sta. Bull.* **323**.
- RUSSELL, H. L., and MORRISON, F. B. 1922. *Ann. Rept. Wisconsin Agr. Expt. Sta. Bull.* **339**.
- SARKAR, B. C. R., LEUCKE, R. W., HUFFMAN, C. F., and DUNCAN, C. W. 1951. The

- chemical composition and nutritive value of yellow dent corn grain. II. The thiamin, riboflavin, niacin and pantothenic acid content. *Michigan Agr. Expt Sta. Quart. Bull.* **33**: 361-371.
- SAUBERLICH, H. E., CHANG, W. Y., and SALMON, W. D. 1953a. The amino acid and protein content of corn as related to variety and nitrogen fertilization. *J. Nutrition* **51**: 241-250.
- SAUBERLICH, H. E., CHANG, W. Y., and SALMON, W. D. 1953b. The comparative nutritive value of corn of high and low protein content for growth in the rat and chick. *J. Nutrition* **51**: 623-635.
- SCHNEIDER, B. H. 1947. Feeds of the world, their digestibility and composition. West Virginia Agr. Expt. Sta., Morgantown.
- SCHNEIDER, B. H., LUCAS, H. L., PAVLECH, H. M., and CIPOLLONI, M. A. 1950. The value of average digestibility data. *J. Animal Sci.* **9**: 373-379.
- SCHNEIDER, B. H., and LUCAS, H. L. 1950. The magnitude of certain gross sources of variability. *J. Animal Sci.* **9**: 504-512.
- SCHNEIDER, B. H., LUCAS, H. L., PAVLECH, H. M., and CIPOLLONI, M. A. 1951. Estimation of the digestibility of feeds from their proximate composition. *J. Animal Sci.* **10**: 706-713.
- SCHNEIDER, B. H., LUCAS, H. L., CIPOLLONI, M. A., and PAVLECH, H. M. 1952. The prediction of digestibility for feeds for which there are only proximate composition data. *J. Animal Sci.* **11**: 77-83.
- SCHNEIDER, B. H., BESSON, K. C., and LUCAS, H. L. 1953a. Nutrient composition—Corn in the United States. *Agr. and Food Chem.* **1**: 172-177.
- SCHNEIDER, B. H., BEESON, K. C., and LUCAS, H. L. 1953b. Composition of corn in the United States 1946-1947. *Natl. Research Council (U. S.), Publ.* **258**.
- SCHNEIDER, E. O., EARLEY, E. B., and DE TURK, E. E. 1952. Nitrogen fractions of the component parts of the corn kernel as affected by selection and soil nitrogen. *Agron. J.* **44**: 161-169.
- SCHULTZ, A. S., ATKIN, L., and FREY, C. N. 1941. A preliminary survey of the vitamin B₁ content of American cereals. *Cereal Chem.* **18**: 106-113.
- SCOTT, H. M., MATTERSON, L. D., and SINGSEN, E. P. 1947. Nutritional factors influencing growth and efficiency of feed utilization. I. The effect of the source of carbohydrate. *Poultry Sci.* **26**: 554.
- SHAWALTER, M. F., and CARR, R. H. 1922. Characteristic proteins in high and low protein corn. *J. Am. Chem. Soc.* **44**: 2019-2023.
- SHEDD, C. K. 1945. Handling and storing soft corn on the farm. *U. S. Dept. Agr. Farmers' Bull.* **1976**.
- SINGAL, S. A., SYDENSTRICKER, V. P., and LITTLEJOHN, J. M. 1947-1948. The role of tryptophane in the nutrition of dogs on nicotinic acid deficient diets. *Federation Proc.* **6**: 422.
- SINGAL, S. A., SYDENSTRICKER, V. P., and LITTLEJOHN, J. M. 1948. The nicotinic acid content of tissues of rats on corn rations. *J. Biol. Chem.* **176**: 1069-1073.
- SNYDER, W. P. 1926. Pork production at the North Platte Substation. Comparison of the relative feeding values of white and yellow corn for fattening hogs. *Nebraska Agr. Expt. Sta. Bull.* **214**.
- SPEER, V. C., CATRON, D. B., HOMEYER, P. G., and CULBERTSON, C. C. 1952. Trace minerals for growing-fattening swine in drylot. *J. Animal Sci.* **11**: 112-117.
- STEENBOCK, H., and BOUTWELL, P. W. 1920. The comparative nutritive value of white and yellow maizes. *J. Biol. Chem.* **41**: 81-96.
- SURE, B. 1948a. The nature of the supplementary value of the protein in milled corn meal and milled wheat flour with dried food yeasts. *J. Nutrition* **36**: 59-63.

- SURE, B. 1948b. Relative supplementary values of dried food yeasts, soybean flour, peanut meal, dried non-fat milk solids, and dried buttermilk to the proteins in milled white corn meal and milled enriched wheat flour. *J. Nutrition* **36**: 65-73.
- SWIFT, R. W., COWAN, R. L., VARRON, G. P., MADDY, K. H., and GROSE, E. C. 1951. The effect of alfalfa ash upon roughage digestion in sheep. *J. Animal Sci.* **10**: 434-438.
- TERRILL, S. W., MOFFITT, J. G., KRIDER, J. L., EARLEY, E. B., and BULL, S. 1951. Value of low and high fat corn for fattening hogs. *J. Animal Sci.* **10**: 902-906.
- U. S. DEPT. AGR. 1934. Official grain standards of the United States. *Service and Regulatory Announcement* **144**.
- VAUGHN, H. W. 1927. Rations for fattening baby beeves and selection of calves for baby beef production. *Minnesota Agr. Expt. Sta. Bull.* **237**.
- VESTAL, C. M., and SHEWSBURY, C. L. 1944. The feeding value of hominy feed for hogs. Its effect on the quality of pork. *Indiana Agr. Expt. Sta. Bull.* **501**.
- WEEKS, M. E., and FERGUS, E. N. 1946. Effects of soil, soil treatment, seasonal variation, and variety on yield and composition of corn crops grown on Kentucky soil fertility plots. *Kentucky Agr. Expt. Sta. Bull.* **485**: 52.
- WILSON, J. W., and BUSHEY, A. L. 1926. Soft corn for fattening cattle. *South Dakota Agr. Expt. Sta. Bull.* **219**.

CHAPTER XVI

The World Production of Corn

G. F. SPRAGUE

The previous chapters in this book have dealt with the general topics of breeding, production, and utilization. Within each category the prime emphasis has been placed on conditions and developments within the United States. This emphasis should not be interpreted as an indication that the importance of corn as a crop is limited to this area. Rather, it was an attempt to restrict coverage to the area where research on corn has received the greatest emphasis. Great progress has also been achieved in other areas of the world. It was necessary to omit most of this information to keep the size of this volume within reasonable limits. The purpose of this chapter is to provide brief information on the important corn-growing areas and production practices of areas outside the United States.

Climate, fertility, production practices, and the genetic limitations of the types grown, each has an important influence on corn production. These factors may differ in importance in the several corn-growing areas.

The word climate is used in a broad sense to include temperature, rainfall, etc. In the Northern Hemisphere corn production reaches its greatest intensity in an area delimited by 70°F. and 80°F. isotherms for July. In parts of this area rainfall distribution becomes a limiting factor. The same general situation prevails in the Southern Hemisphere when due allowance is made for the reversal in growing seasons. It is only in those areas where both temperature and rainfall distribution are favorable that total corn production is high.

Data on corn acreage, yield in bushels per acre, and production for specified countries for the postwar period are presented in Table I. It may be of some interest to attempt to relate some of these marked differences in acreage and production to climatic conditions. Corn production reaches its greatest intensity in the corn belt of the United States. This region is characterized by mean temperatures, during July, lying between 70°F. and 80°F., the period of silking and tasseling. Average rainfall during the growing season ranges from 10 to 20 inches with a frost-free period in excess of 130 days.

CORN ACREAGE, YIELD PER ACRE, AND PRODUCTION IN SPECIFIED COUNTRIES 1945-1949 AVERAGE AND 1951-1953 ANNUAL

TABLE I

Continent and country	Acreage, in thousands of acres				Yield per acre, in bushels				Production, in thousands of bushels			
	1945-49	1951	1952	1953	1945-49	1951	1952	1953	1945-49	1951	1952	1953
North America												
Canada	238	314	339	362	45.2	50.9	58.2	57.6	10,755	15,990	19,722	20,854
Cuba	433	440	380	—	16.2	16.1	15.8	—	7,011	7,100	6,000	—
Guatemala	1,208	1,375	1,375	—	14.9	13.1	13.1	—	17,991	18,000	18,000	20,000
Mexico	8,694	10,940	10,470	11,120	10.7	12.3	12.0	11.3	95,389	135,000	126,060	125,970
Nicaragua	174	240	303	252	16.0	15.0	14.1	13.5	2,782	3,600	4,280	3,390
United States	85,696	80,736	81,099	80,279	35.7	35.9	40.4	39.6	3,056,861	2,899,169	3,279,403	3,176,615
Europe												
Austria	152	160	150	160	39.2	25.5	34.4	32.3	3,870	5,500	4,850	5,900
France	649	863	862	920	16.2	31.5	22.1	33.6	10,491	27,180	19,090	30,870
Greece	582	624	625	645	14.7	15.8	14.5	18.6	8,564	9,840	9,060	12,000
Italy	3,250	3,300	3,310	3,350	28.0	35.8	30.8	37.3	90,980	118,000	102,000	125,000
Portugal	1,238	1,130	1,230	1,210	10.0	15.0	14.6	10.3	12,368	16,940	17,930	12,410
Spain	926	990	1,000	1,025	21.5	25.9	27.0	25.4	19,920	25,600	27,000	26,000
Asia												
China	12,711	12,100	12,200	—	21.6	20.7	21.3	—	274,031	250,000	260,000	—
India	7,761	7,960	8,800	8,500	10.3	10.0	11.8	—	79,836	79,500	104,000	—
Japan	133	160	168	173	21.7	25.1	27.6	22.5	2,881	4,020	4,630	3,900
Manchuria	6,680	7,500	7,650	—	19.5	20.7	21.6	—	130,000	155,000	165,000	—
Pakistan	986	960	970	1,067	16.9	16.7	15.5	16.4	16,688	16,000	15,000	17,480
Philippine Rep.	1,820	2,645	2,721	—	10.1	11.3	10.4	—	18,340	29,840	28,420	29,920
Turkey	1,394	1,540	1,586	1,530	16.1	21.7	20.8	21.7	22,406	33,460	32,950	33,266

TABLE I (Continued)

Continent and country	Acreage, in thousands of acres				Yield per acre, in bushels				Production in thousands of bushels			
	1945-49	1951	1952	1953	1945-49	1951	1952	1953	1945-49	1951	1952	1953
Africa												
Egypt	1,699	1,720	1,770	2,090	33.4	32.6	33.5	34.9	56,696	56,000	59,300	73,000
French Morocco	1,260	1,245	1,165	1,254	8.0	6.8	9.8	8.8	10,074	8,500	11,400	11,000
“ West Africa	—	1,523	1,516	—	—	8.7	8.7	—	—	13,240	13,200	—
South Rhodesia	293	361	390	—	18.1	24.4	23.1	—	5,298	5,800	9,000	—
Union S. Africa	7,106	6,510	8,040	8,780	12.2	11.3	14.8	14.6	86,699	73,390	118,750	128,500
South America												
Argentina	5,363	3,536	5,919	7,700	28.9	22.7	23.6	30.5	155,012	80,310	139,760	235,000
Brazil	10,866	11,740	12,125	12,500	20.7	19.8	19.2	19.2	224,400	233,000	232,500	240,000
Chile	115	150	126	—	22.5	23.3	28.2	—	2,589	3,500	3,550	—
Colombia	1,654	1,898	2,086	2,086	15.4	17.5	17.5	18.9	25,429	33,270	36,530	39,400
Uruguay	395	641	725	—	10.1	7.2	11.9	—	3,997	4,610	8,592	—
Oceania												
Australia	222	170	141	167	26.6	23.6	29.4	25.4	5,899	4,020	4,150	4,240
New Zealand	7	6	6	6	55.6	63.3	58.3	58.3	389	380	350	350
Estimate World Total	213,720	213,210	219,480	222,790	—	—	—	—	5,275,000	5,280,000	5,630,000	5,575,000

In the Northern Hemisphere, Portugal, part of Spain, southern France, Italy, Switzerland, the Balkans, Greece, and large areas of the U.S.S.R., China, and Manchuria lie within the temperature limits listed above. However, the corn belt of Europe includes only the Eastern Danube plains area of the Balkans and from the Po Valley north to the foothills of the Alps in Italy and Switzerland. In other areas having a satisfactory summer temperature, rainfall is either inadequate or its distribution is too erratic for corn to be a reliable crop. In France the production of corn for grain reaches its greatest intensity in the southwestern and central areas. Here temperatures are favorable, but rainfall is often limiting. In southern Italy and Greece, rainfall and low soil fertility are both limiting factors. In the Macedonian plains of northern Greece, rainfall is both more abundant and less erratic, and it is in this area that Greek corn production reaches its maximum.

Using the mean July temperature of 70°F. as the northern limit for the effective production of grain, northern France, Holland, Belgium, and Germany would be expected to grow little corn for grain. This has been the pattern in the past. However, it has been found since World War II that short-season American hybrids will produce economically competitive yields of corn in at least some parts of these countries. These satisfactory yields are obtained in spite of the obvious poor adaptation of these hybrids. Presumably the most important factor making for poor adaptation of the American hybrids is their inability to grow at low temperatures. Adapted local varieties grow well during the early part of the growing season when the weather is cool, whereas the American hybrids remain yellow and stunted during this period. As temperatures increase during late June and July, the hybrids exhibit an increase in growth rate and eventually produce yields 25 to 50 per cent in excess of the local varieties. When suitable hybrids are developed from local material it appears logical to assume that even greater increases in yield will be attained. Observational evidence now available indicates that some of the local strains grown in northern Europe have an appreciably lower temperature requirement than the corns commonly grown in northern United States and southern Canada.

In Asia, Turkey, large areas of the U.S.S.R., China, and Manchuria lie within the area delimited by the 70°F. to 80°F. July isotherms. Toward the northern limit of this area corn is of limited importance because of inadequate rainfall. Both China and Manchuria produce large amounts of corn with production concentrated in eastern sections where the total rainfall and the distribution pattern are more favorable. Turkey lies near the 80°F. isotherm. Corn production reaches its greatest concentration along the Black Sea and the Mediterranean, where rain-

fall is adequate. Corn production is of limited importance in Japan, which lies partially within the proscribed temperature range.

In the Southern Hemisphere, the important corn-growing areas of Argentina and southern Brazil lie within the 70°F. to 80°F. isotherms for January. The Union of South Africa is the largest corn-producing country in Africa, but only a small portion of this country lies within the specified temperature limits.

Argentina and Brazil are the largest producers of corn in the Southern Hemisphere. Most of the corn grown in Brazil is consumed locally, whereas Argentina is one of the largest exporters of corn. The corn-growing area of Argentina is located fairly close to the sea coast, which gives it a decided advantage in shipping as compared to the corn belt of the United States. Rainfall distribution in Argentina is somewhat erratic, and prolonged periods of heavy rainfall often occur during the harvest season, which increases the incidence of ear rots. Flint corn is the type commonly grown, possibly because of its greater suitability for ocean transport and because of its greater resistance to ear rots.

Northern South America, Central America, Egypt, India, and the Philippines lie within an area where temperatures are less favorable for maximum yield, at least as judged by conditions prevailing in the corn belt of the United States. In some areas elevation permits more favorable temperature conditions than would be expected on the basis of latitude. This is partially true of the Central Mesa of Mexico, which is also the area of greatest corn production. A much smaller but still important production area of Mexico occurs in the Gulf Coastal plains.

Corn is not an important crop in India, occupying less than 5 per cent of the cropped land. Acreage and production per acre are greatest in the middle Ganges area. Corn is also grown in the Punjab area of Pakistan.

In the Philippines, corn ranks next to rice as a subsistence crop. The culture of corn is most important in the Cagayan Valley of northern Luzon and in the lowlands of Bohol, Cebu, and eastern Negros.

This central area lying between the corn belts of the United States and Europe, on the north, and the corn belt of southern Brazil and Argentina, on the south, is characterized by low average yields per acre. The one notable exception to this generality is Egypt. Low average yields throughout this general region may be caused by some combination of the following factors: low soil fertility, suboptimal climatic conditions, poor cultural practices, and genetically inferior varieties.

I. Soil Fertility

Soils in the tropics are characterized by low fertility and low organic matter. Fertilization and crop management practices are often inade-

quate, and the soils have been under cultivation for long periods of time. Under such conditions yields are expected to be low and erratic and hybrids may exhibit little superiority under such conditions. However, given adequate fertility, management, and cultural practices the differences in yield between local varieties and adapted hybrids may be very striking.

II. Climatic Limitations

Suboptimal climatic conditions may include several factors. One of the most important factors is rainfall, both in amount and distribution. High rainfall and humidity may have an adverse effect on growth and pollination and may also increase the incidence of various blights, mildews, etc. Excessive rainfall may also result in leaching of nutrients from the soil and result in a waterlogged condition which limits normal nitrification.

Inadequate precipitation or poor rainfall distribution will also have an adverse effect on yield. Under extreme conditions the leaf tissue may be killed by either inadequate moisture or excessive heat. The combination of heat and drought during pollination may result in poor seed setting or in a complete failure of seed setting and therefore reduced yields.

The alternation of seasons involving pronounced changes in temperature or rainfall plays a very important role in the control of plant pathogens and insect pests. The absence of such periodic control is undoubtedly a factor of considerable importance in limiting yields in some of the tropical and semitropical lowlands.

III. Cultural Practices

Cultural practices for the production of corn vary from a high degree of mechanization to a primitive type of agriculture making extensive use of hand tools and wooden plows. In the areas of extensive mechanization, special machinery has been developed for planting, cultivating, and harvesting the corn crop. In other areas where corn culture is less important, machines designed for the planting of other crops are modified for corn planting. In parts of Europe, grain drills or sugar-beet drills are often used for planting corn. In other areas corn may be planted by hand or sown broadcast and plowed under with a wooden plow. Obviously under such conditions no cultivation other than hand hoeing is possible. Seed requirements are high, and resulting yields are usually low.

Planting rates vary widely in different areas of the world. Average plant population for parts of South Africa and for southern Italy are 7000 to 8000 plants per acre, for the corn belt area of the United States

about 12,000 to 16,000 plants, and for some areas of western Europe, 20,000 to 30,000 plants per acre. Furthermore, extensive experimentation has demonstrated that such population densities are close to optimum for these respective areas. The low population density for South Africa can be easily accounted for by the periodic droughts preceding or following the pollination period. No equally obvious explanation has been advanced to account for the differences in optimum stand densities in the other two areas.

The machinery available for planting types of corn and local customs have a pronounced influence on acceptable seed sizes. In the Union of South Africa, all seed passing through a No. 24 screen is discarded as too small for seed. In the United States, all corn remaining on a 24 screen is discarded as being too large to plant. In both the United States and the Union of South Africa, the "flat" sizes of seed command a premium and "round" sizes sell at a reduced price. In some other areas this prejudice against round sizes is not encountered.

In earlier years it was a common practice in the southern part of the United States to top corn, *i.e.*, to remove the stalk and leaves above the ear some time after pollination. This practice is still followed to some extent in parts of western Europe. It is generally recognized that this practice leads to reduced yields, the magnitude of the reduction being influenced by the stage of development at the time of topping.

Harvesting procedures are as diverse as planting methods. In the Union of South Africa, corn is left in the field until the moisture content has dropped to 15 to 16 per cent. As a consequence of the long field storage period the incidence of ear rots is high. At the other extreme corn is harvested at a moisture percentage of 30 to 35 in northern France and Holland. The corn may be husked in the field and stored in narrow cribs or may be combined and the wet shelled grain dried artificially. Some success has also been had with shelling of snapped corn with an ordinary threshing machine, operated at slower than normal speed. Drying of small grains is a common practice in this area, and the drying equipment available can be modified to handle shelled corn. The drying period required is considerably longer than for small grains because of the higher moisture percentage.

IV. Progress in Corn Breeding

Corn is used for different purposes in various areas of the world. The three primary uses are: (1) as grain for livestock feed, (2) as a silage or green fodder crop, and (3) as human food. No critical information is available, but it appears entirely reasonable to assume that these primary uses have had a direct or indirect effect on yield.

In the areas where corn is grown primarily for human food (Central America, and parts of South America, Europe, Africa, and Asia), the individual fields are usually small in area, and seed is saved from such plantings for the following crop. The combination of small fields and the saving of small seed lots from these plantings would be expected to result in considerable inbreeding over a period of years. This inbreeding, in spite of any selection practiced, would be expected to result in appreciable yield reductions. The reduced yield level due to inbreeding may account for the relative ease in obtaining increased yields by the introduction of new and presumably less well-adapted types.

In many areas of western Europe, corn has been used largely as a silage or green fodder crop. Where this usage has been common, the bulk of the seed has been imported from other areas, *e.g.*, the western Balkans area has supplied seed for areas of western Europe. Under such conditions after a suitable maturity type has been identified, changes in seed source have been minor. Improvement in silage or green fodder yields would be primarily the result of improvements in fertilization and cultural practices rather than of genetic improvement in the types grown.

Major emphasis on improvement of varieties through breeding has been in those areas where corn is grown primarily for grain as a livestock feed. Under such conditions the fields are large and the quantities of seed required for planting are also large, which minimizes any inbreeding depression effect. It is also in the areas of large-scale production that the utilization of hybrids has been most widespread.

The improvement of corn by inbreeding and hybridization is receiving attention in many parts of the world. Breeding investigations at the Connecticut and the Nebraska experiment stations were started before 1910 and have been continued to the present time. Most of the breeding programs of the corn belt area of the United States were started about 1920. Some idea of the scope of the breeding work is presented in Chapter V.

Breeding work was started in Argentina in the 1920's, but was interrupted before commercially usable hybrids were developed. Work was started in Egypt, Portugal, Spain, and Brazil in the 1930's. Many of the European programs have been started since the end of World War II and have received considerable financial or technical assistance from one or more of the following agencies: United Nations Relief and Rehabilitation Agency, Economic Co-operation Administration, and Mutual Security Administration. These programs have been successful to varying degrees.

Breeding programs in various parts of the world differ in the methods used, in the diversity of parental material available, and in the

amount of governmental regulation or control. In the section that follows an attempt will be made to cite specific examples illustrative of differences among programs rather than to consider all programs in detail.

The breeding program in Italy was started about 1920. Most of the original material was lost during World War II, and the program was revised and expanded after that period. They have been particularly fortunate in that the important corn area of Italy, the Po Valley, can make effective use of United States hybrids and inbred lines of corn belt maturity. In southern Italy, early maturity and drought resistance are attributes of prime importance. Corn is planted in early summer after the removal of a wheat crop or the first cutting of hay. Most of the rain is received during the winter months and the corn crop must be produced almost entirely on stored soil moisture. The native varieties adapted to this area are flints. Experimental flint $\times$ dent combinations appear to offer considerable promise for this area of Italy. Locally developed hybrids have not come into general use because facilities for the production of seed stocks are limited.

Hybrid corn may eventually play an important role in the agricultural economy of France. In the past, the production of corn for grain has been largely confined to southern and central France. Since the war, corn production has been tried on a limited scale in northern France, with promising results. All but the earliest of United States hybrids are too late for this area, and maximum production will only be achieved when locally developed hybrids become available. France has adopted a strict policy on the importation of hybrid seed that appears to have had a harmful rather than beneficial effect. Until this policy is modified, France will be dependent upon hybrids involving either released United States lines or lines of their own development. Thus far locally developed hybrids have not played an important role. Here, as in several other of the European countries, progress will be largely dependent upon the development of adequate provisions for the production of foundation single crosses.

Holland has made tremendous progress in the utilization of hybrids since the war. Prior to that time, the corn acreage of Holland did not exceed 1000 hectares (2500 acres). Officials estimate that eventually the acreage may increase to 70,000 hectares. In the past, rye has been an important crop on the sandy soils of the country. Hybrid corn is rapidly replacing rye in these areas, with a substantial increase in total yield. Short-season hybrids from the United States and Canada are being produced locally. Locally developed hybrids of flint-dent parentage are being used and appear to be better adapted and produce higher yields than the short-season corn belt material. Commercial breeding

and seed production is in the hands of private seed companies. The University of Wageningen contributes to the total program by fundamental studies on breeding and production practices.

The corn-breeding program in Mexico, sponsored jointly by the Rockefeller Foundation and the Mexican Government, was initiated in 1944. In the early stages of the program high-yielding open-pollinated varieties were identified and distributed. Later, emphasis was shifted to top-cross combinations and finally to double crosses. The quantity of double-cross seed distributed in 1954 exceeded 6000 tons. This program is unique in the effective use which has been made of early testing and the use of superior S_1 lines in hybrid combinations. This practice was initially adopted in order to distribute improved types to the farmers as quickly as possible. Data obtained subsequently have indicated that double crosses produced from S_1 parental lines have essentially the same yielding ability as double crosses produced from inbred lines representing three to five generations of inbreeding. The use of S_1 lines introduces important problems in maintaining the genetic purity of parent seed stocks. However, judging by the continued high level of performance of the double crosses now being produced commercially, these problems appear to have been satisfactorily solved. At the present time the Mexican Maize Commission is responsible for the production and distribution of all hybrid seed produced.

Double-cross hybrids have been produced and are now commercially available in the states of Minas Gerais, São Paulo, and Rio Grande de Sul in Brazil. Private and public agencies have been active in both breeding and seed production. Dent $\times$ flint and all flint combinations are commercially available. The utilization of hybrid corn may be expected to increase as facilities for production are increased and as facilities for transportation are improved.

Corn breeding has been undertaken in many countries. In some, marked progress has been made as indicated above. In others, either breeding has not been attempted or the programs are still too young to have demonstrated their value. In every country where a serious attempt has been made to improve corn by inbreeding and hybridization, the efforts have been successful.

Techniques of breeding and procedures for seed stock production have been developed and evaluated in the many breeding programs in the United States. Other countries, following these patterns, should be able to progress at a more rapid rate than that which characterized the initial stages of hybrid corn development in the United States. Improved techniques of breeding and production together with improved rotation and fertilizer practices should enable corn to play a much more important role in world agriculture than it has up to the present time.

INDEX

A

Acetic acid, 634
 Acetone, 632
Aeolothrips fasciatus, 592
 femoralis, 592
Aeolus mellillus, 548
Aerobacter aerogenes, 632
Agonoderus lecontei, 558
Agriotes mancus, 548
Agrostis gladiara, 546
Agrostis ypsilon, 546
Ahasverus advena, 601
 Alcohol,
 butyl, 632
 ethyl, 629
 Alloploidy, 22
 Aluminum in leaf tissue, 305, 307
 Amino acids, 626
 Amylopectin, 280, 618
 Amylose, 280, 618
 Anaphase configurations, 158, 184
Anaphothrips obscurus, 592
 Andropogoneae, 9, 14, 17, 21
 Aneuploidy, 134
Angiospora zae, 510
 Angoumois grain moth, 599
 Anthracnose, 515
Anuraphis maidi-radici, 554
 Aphid, corn root, 554
 leaf, 587
Aphis gossypii, 521, 594
Aphis maidis, 275, 521, 594
Aplanobacter stewartii, 593
 Armyworm, 578
 chemical control, 580
 fall, 571
 control, 573
 habits and biology, 573
 varietal resistance, 573
 habits and biology, 579
Aspergillus flavus, 469, 661
Aspergillus glaucus, 662
 Autoploidy, 22
 and perennial growth habit, 26, 27

B

B chromosomes, 127, 138
 Backcrossing, 239
 Bacterial diseases, 593
 Bacterial leaf blight, 512
 Bacterial stalk rot, 481, 512
 Bacterial wilt, 499
 inheritance of resistance, 504
 resistant lines, 505
Bacterium aceti, 634
Bacterium stewartii, 277, 502
Baldulus elimatus, 522, 595
Baldulus maidis, 522, 595
 Beetle, flour, 599, 601
 grain, 601
 hairy fungus, 601
 Billbugs, 550
 Black bundle disease, 526
Blissus leucopterus, 274, 581
 Boron in leaf tissue, 304, 307, 310
 Brewer's flakes, 629
 Brown spot, 510
 Butyl alcohol, 632
 Butylene glycol, 631

C

Cadelle, 598
 Calcium percentage,
 in leaves, 296, 303, 307
 in stems, 297
 in whole plant, 299, 301
Calendra callosa, 550
 destructor, 550
 maidis, 550
 parvula, 550
 zae, 550
 Carotene, 651, 654
 Caryopsis, development of, 63-74
 Centromeres, 142
Cephalosporium acremonium, 526, 593
Cercospora zae-maydis, 515
 Certification, role of, 380

- Chaetocnema denticulata*, 500, 593
Chaetocnema pulicaria, 500, 589, 593
 Charcoal rot, 477
Chelonus annulipes, 569
 Chemical composition,
 breeding for, 279
 Chiasmata, 144, 149
 Chinch bug, 581
 barriers, 584
 cultural practices, 583
 habits and biology, 582
 varietal resistance, 583
 Chlamydospores, 517
 Choline, 627, 645
 Chromatid interference, 154, 158, 187
 Chromatids, 145, 151
 Chromosome,
 abnormal 10, 130, 197
 non-disjunction, 177
 Chromosome bridges, 158, 185, 193
 Chromosome knob number,
 corn, 33, 40, 125
 relation to altitude, 39
 relation to plant characters, 39, 40
 teosinte, 30
 Tripsacum, 36
 maizar, 37
 zopilotense, 38
 Chromosome morphology, 28, 124, 126
 Chromosome numbers, corn and its rela-
 tives, 18-22
 Chromosome pairing, 142
 Chromosomes, B type, 127
 morphological differences among *Zea*,
 Euchlaena and *Tripsacum*, 28-33
 pachytene, 140
 ring, 132, 195
 telocentric, 137
Cicadulina dipunctella, 594
 mbila, 594
 storeyi, 594
 Cleaning seed corn, 405
 Climatic limitations, 326, 684
Clivina impressifrons, 558
Clostridium acetobutylicum, 633
Clostridium polymyza, 632
 Cob structure, 97
 Cobalt, in leaf tissue, 309
Cochliobolus heterostrophus, 495
 Coix, 18, 501
Colaspis flavida, 557
 Cold test, 413, 472
 Cold test germination, 401, 412
Coleomegilla maculata, 588
Colletotrichum graminicola, 515
Commelina nudiflora, 594
 Composition, kernel parts, 661
 Composition of tissue, 294
 Convergent improvement, 239
 Conversion tables, dry weight, 399
 Copper, in leaf tissue, 305, 307
 Corn, abnormal chromosome 10, 197-201
 anomalous ears, 115-119
 B chromosomes, 138-139
 breeding, 221-283
 pre-Mendelian, 3
 progress, 685
 chemical composition of, 639
 chromosome morphology, 124-131
 chromosome numbers, 18
 climatic requirement, 315-339, 679-
 682
 cold tolerance, 321, 325
 crossing over in, 147-169
 cultivation, 365-367
 culture, 343-375
 cytogenetic aspects of origin, 16-57
 cytoplasmic sterility, 269-272
 deficiencies, 192-195
 development of flower and inflores-
 cence, 97-102
 of modern America, 3
 diseases, 465-527
 control, 467-469
 insects in relation to, 592-595
 of leaf, 492-515
 resistance, 275-278
 distribution, pre-Columbian, 4, 5
 divergent evolution, 14-16
 domestication time of, 16
 dry milling, 627-629
 ear rots, 482-492
 ear-to-row selection, 228-233
 early history of, 1-9
 energy content of, 668-669
 establishment in old world, 2
 evaluation of inbred lines, 245-251
 farm drying and storage, 372-375
 fermentation industries, 629-634
 floral abnormalities in, 110-115
 gametophytes and fertilization, 103-
 105

- genetic modification of chemical composition, 279-282
- grades, 642
- hybrid seed production, 379-418
- immature, 641
- industrial utilization, 613-634
- inflorescences, 90-97
- insect pests, 537-603
- insect resistance, 272-275
- intercropping, 362-364
- inversions, 183-192
- irrigation, 367-372
- leaf diseases, 492-515
- leaf, stalk and ear insects, 558-592
- lime and fertilizer requirements, 349-355
- mass selection, 221-225
- meiosis, 139-147
- mineral composition, 647
 - calcium and sodium deficiencies, 648
 - manganese, 650
- mineral nutrition of, 293-313
- moisture content in relation to feeding value, 640-642
- multiple hybrids and synthetics, 254-257
- mutations, 201-212
- nurse crop, 362
- nutritive value of, 637-670
 - disease and, 661, 662
 - of ground, 664-667
- origin theories, 6
 - Africa, 7
 - American, 8
 - Asia, 7
 - divergent evolution, 14
 - Herbalists, 6
 - Hybrid, 11
- pellagra and, 646, 647
- place of origin, 15
- planting, 355-362
- polyploidy, 131-138
- pre-Columbian America, 4
 - distribution, 5
 - varieties and uses, 5
- prediction of double cross performance, 251-254
- production, climate and, 315-318
 - regions of, 316
- protein content, 642-646
- recurrent selection, 257-263
 - relatives, 9-14
 - ring chromosomes, 195-197
 - seed and seedling diseases, 469-472
 - selection of inbred lines, 233-245
 - smuts, 515-520
 - common, 516
 - head smut, 519
 - soil insects, 539-558
 - soil requirements, 344-345
 - spikelet and flower, 89-90
 - stalk and root rots, 473-482
 - stored grain insects, 595-602
 - translocations, 169-182
 - types of gene action, 263-269
 - varietal hybridization, 225-228
 - vitamin composition, 651
 - wet milling, 613-627
 - wild ancestor of, 14
 - world production of, 315-318, 679-688
 - yellow vs. white, 652
- Corn and cob meal, 665
- Corn borer, European, 564
 - biological control, 568
 - chemical control, 570
 - cultural practices, 570
 - habits and biology, 566
 - varietal resistance, 569
- Corn borers, southern, 574
 - cultural practices, 578
 - habits and biology, 576
- Corn borer parasites, 569
- Corn borer predators, 569
- Corn flea beetle, 456, 589
- Corn flour, 629
- Corn grass, 112
- Corn meal, 629, 663
- Corn mosaic, 520
- Corn nutrient correlations, 659
- Corn oil, 624
- Corn rootworm, 539
 - southern, 544
- Corn season, ideal, 334
- Corn shows, 224
- Corn stunt, 521
- Corn sugars, 623
- Corn syrup, 623
- Corn $\times$ teosinte hybrids, 43, 44
 - linkage relations in, 32
- Corn $\times$ tripsacum hybrids, 11, 17, 47
- Corn-wheat sequence, 364
- Corn worm, pink, 601

- Correlation between characters, 241
 - Crambus caliginosellus*, 551
 - mutabilis*, 551
 - trisectus*, 551
 - Crop rotation, 468
 - Cropping system, 348
 - Cross sterility, popcorn, 435
 - Crossability, corn and related species, 41-53
 - corn and *Tripsacum*, 41, 47, 49
 - Crossing over,
 - chromatid, 150-152
 - cytologic and genetic, 147
 - in males and females, 167
 - post diplotene association, 149
 - sister strand, 156, 159
 - variability in, 165
 - Crossover distribution, 162
 - Crossovers,
 - unequal distribution of, 162
 - Crymodes devastator*, 546
 - Cultivation, 365
 - Cultural operations, cost of, 343, 345
 - Cultural practices, 684
 - Cutworms, 546
 - cultural practices, 547
 - habits and biology, 547
 - Cynaëus angustus*, 601
 - Cytological location of genes, 159, 191
 - Cytoplasmic sterility, 269, 392
- D**
- Deficiencies, chromosomal, 160, 192, 196
 - Deficiency symptoms, nutritional, 354
 - Detasseling costs, 391
 - Detasseling seed fields, 387
 - crew, 388
 - contract, 389
 - machine, 389
 - Detasseling standards, 390
 - Dextrose, 623
 - Diabrotica longicornis*, 274, 500, 539
 - Diabrotica undecimpunctata*, 274, 500, 544, 593
 - Diabrotica virgifera*, 543
 - Diatraea crambidoides*, 574, 577
 - grandiosella*, 574, 577
 - Diplodia ear rot, 482
 - Diplodia frumenti*, 490
 - Diplodia macrospora*, 491
 - Diplodia stalk rot, 474
 - mode of infection, 474
 - resistance to, 476
 - spores, 474
 - symptoms, 473
 - Diplodia zeae*, 276, 469, 474, 476, 483, 593, 661
 - Disease and nutritive value, 661
 - Disease control,
 - development of resistant hybrids, 467
 - use of fungicides, 468
 - Disease development,
 - factors affecting, 465
 - disease inciting agent, 467
 - environment, 466
 - host resistance, 466
 - Disease resistance, breeding for, 275
 - diplodia stalk rot, 276
 - leaf blights, 277
 - smut, 278
 - Distillation, fractional, 630
 - Distillers grains, 631
 - Dominance, degree of, 266, 267
 - Dominance hypothesis, 263
 - Double cross prediction, 251
 - Downy mildews, 523
 - Drainage, 347
 - Drosophila*, 20, 151, 154, 186, 191
 - Drought intensity, measure, 331, 332
 - Dry matter,
 - leaves, 296, 303
 - stems, 297
 - whole plant, 299, 301
 - Dry milling, 627
 - flow chart, 628
 - Drying seed corn, 401
 - Drying temperatures for seed, 402
 - Duplications, chromosomal, 161, 196
 - intrachromosomal, 20
- E**
- Ear, anomalies, 115
 - row number, 117, 118
 - Ear-to-row selection, 228
 - chemical composition, 230
 - plant and ear height, 231
 - yield, 232
 - Early testing, 238
 - Earworm, corn, 558
 - cultural practices, 564

habits and biology, 559
 varietal resistance, 562
Elasmopalpus lignosellus, 580
Eleusine coracana, 525
 Embryology, 63, 109
 Energy content, cereals, 668
Erwinia dissolvens, 481
 Ethyl alcohol, 629
Euchlaena, 501, 524
 mexicana, 18, 26, 105, 512
 perennis, 18, 26, 27
Euetheola rugiceps, 556

F

Feltis subgothica, 546
 Fermentation products, 629
 Fertilization, 104, 109
 preferential, 177
 Fertilizer requirements, 349
 Flame weeding, 367
 Flea beetle, corn, 456, 589
 chemical control, 591
 habits and biology, 590
 Floral abnormalities, 110
 Floral structure,
 cob, 97
 development of flowers, 98
 of spikelets, 98
 ear, 96
 female spikelets, 90
 inflorescence, 90, 92
 male spikelet, 89
 Flour beetle, 599
 larger black, 601
 Fractional distillation, 630
Franklinella tenuicornis, 592
 Freezing injury to seed, 396
 Fungus diseases, 593
 Fusarium kernel rot, 486
Fusarium moniliforme, 471, 486, 593,
 661
 Fusel oil, 630

G

Gamete selection, 240
 Gasteria, 154
 Gene action, types of, 263
 additive, 249, 252, 256, 261

 non-additive, 252, 261
 General combining ability, 248, 260, 433
 Genes, dominant, 124
 duplicate, 20
 polymeric, 20
 Genetic correlations, 242, 243
 Genetic diversity, 246
 Genetic map length, 163
 Germination, 75
 Gibberella ear rot, 484
Gibberella fujikuroi, 471, 486
Gibberella saubinetii, 276
 Gibberella stalk rot, 477
Gibberella zeae, 469, 472, 473, 485, 593
 Gluten corn, 617, 625
 Gluten feed, 625
 Gluten meal, 625
 Glycerol, 634
 Grain beetle, flat, 597
 foreign, 601
 saw-toothed, 598
 Granary weevil, 597
 Grape colaspis, 557
 Grasshoppers, 584
 chemical control, 586
 habits and biology, 585
 Gray ear rot, 488, 489
 Growth, ideal conditions for, 534
 stages of corn, 325

H

Harvest and plant operations, 394
 Harvesting corn,
 mechanical pickers, 369
 picker-shellors, 370
 silage, 370
 Heat units and rate of growth, 386
Heliothis armigera, 274, 558
 Helminthosporium,
 sources of resistance to, 494
Helminthosporium carbonum, 179, 277,
 497
 Helminthosporium leaf spot, 497
 physiologic specialization, 497
 resistant strains, 498
Helminthosporium maydis, 495, 496
Helminthosporium rostratum, 515
Helminthosporium turcicum, 277, 444,
 493

- Herbals, 2
 Herbicides, 366
 Heterofertilization, 169
 Heterosis, 263, 268
Hippodamia convergens, 588
 Histology vegetative plant body, 75-87
Holcus, 524
 Hominy, pearl, 629
 Homozygous diploids, 236
Horistonotus uhlerii, 548
Horogenes punctorius, 569
 Hybrid seed industry, 381
 Hybrids, choice of, 364
 Hydrol, 625
Hylemya cilirura, 555
Hysteroneura setariae, 521
- I
- Inbred increase, 382
 Inbred lines, development of, 234
 convergent improvement and back-
 crossing, 239
 early testing, 238
 gamete selection, 240
 homozygous diploids, 236
 pedigree selection, 235
 single hill method, 235
 standard method, 234
 evaluation of, 245
 Inbred $\times$ variety cross, 245
 Indian meal moth, 600
 Indoleacetic acid, 282
 Inflorescence,
 female, 94
 male, 92
 Inheritance of combining ability, 246
 Inositol, 627
 Insect control in seed fields, 387
 Insect resistance, breeding for, 272
 corn earworm, 274
 European corn borer, 272
 rootworm, 274
 Insects, leaf stalk and ear, 558
 Interactions,
 hybrid $\times$ location, 250
 hybrid $\times$ year, 250
 line $\times$ tester, 247
 Intercropping, 362
 Inversions, 130, 152
 crossing over in, 186
 paracentric, 183
 pericentric, 190
 pollen abortion in, 191
 Iron in leaf tissue, 304, 307
 Irrigation, 367
 Isolation of seed fields, 383
 Isoleucine, 281, 644
- J
- Japanese beetle, 591
- K
- Kernel morphology,
 coleoptile, 68
 embryo development, 63
 endosperm, 73
 integuments, 73
 leaf primordium, 64, 65
 nucellus, 73
 pericarp, 73
 plumule, 68
 proembryo, 63
 radicle, 69
 root-stem axis, 72
 scutellum, 70, 72
 Knob material, 127
 Knob number, 22, 23
 corn, 33, 40, 125
 relation to altitude, 39
 relation to plant characters, 39, 40
 teosinte, 30
 tripsacum, 36-38
- L
- Lactic acid, 633
 bacteria, 630
Laemophloeus pusillus, 597
Laphygma frugiperda, 571
 Leaf aphid, corn, 587
 varietal resistance, 589
 Leaf blight, northern, 492
 southern, 495
 Leaf fleck, 522
 Leafhoppers, 592
 Leaf pulling and yield, 392
 Leaf rust, 506
 Leucine, 281, 644
 Lime requirements, 349

Linkage,
 corn $\times$ teosinte hybrids, 31, 32
 Linkage map, 148
Lydeella stabulans grisescens, 569
 Lysine, 282, 645
Lysiphlebus testaceipes, 588

M

Macrocentrus gifuensis, 569
Macrophoma phaseoli, 478
Macrophoma zae, 488
 Magnesium percentage,
 in leaves, 296, 304, 307
 in stems, 297
 in whole plants, 299, 301
 Manganese in leaf tissue, 305, 307, 310
Manisuris cylindrica, 18, 21
 Mass selection, 221
 popping expansion, 432
 Maturity and seed quality, 397
Maydeae, American, 9, 14, 17, 21, 52,
 105
 Oriental, 18
 other than corn, 105-110
 Meiosis, 139
 anaphase I, II, 146
 diakinesis, 145
 diptonema, 144
 leptotene, 140
 metaphase I bivalents, 145
 metaphase II, 146
 pachynema, 144
 prophase II, 146
 zygonema, 142
Melanoplus bivittatus, 275, 585
Melanoplus differentialis, 275, 584
Melanoplus femur-rubrum, 585
Melanoplus mexicanus, 585
Melanotus communis, 548
Melanotus cribulosus, 548
 Methionine, 645
 Mineral accumulation,
 during growth and development, 294,
 298
 in leaves, 301, 303
 minor elements, 302
 Mold powder, 630
 Monoploids, 131, 143
Mucor sp., 661
 Mulch tillage, 357

Multiple hybrids, 254
 Mutation, 201
 activator, 203
 dissociation, 203
 dotted, 202
 enhancer, 207
 effects of ionizing radiation, 208
 modulator, 206
 mutable loci, 204
Myzus persicae, 595

N

Neocentromeres, 200
Neurospora, 154
 Niacin, 282, 645, 655
 Nicotinic acid, 647
Nigrospora cob rob, 486
Nigrospora arylae, 470, 487, 661
Nigrospora spp., 593
 Nitrogen fertilization, 351
 Nitrogen percentage,
 in leaves, 296
 in stems, 297
 in whole plant, 299, 301
 Non-disjunction, 139
 Non-homologous pairing, 143
 Nucleolar organizer, 128, 173
 Nutrient requirements, 350
 nitrogen, 351
 phosphorus, 354
 potassium, 354
 Nutritive value of diseased corn, 661

O

Octoploids, 133
 Oil extraction, 624, 628
 Oil percentage, selection for, 228, 230
 Oil refining, 625
 Order of pairing lines, 253
 Organic matter, 349
 Origin of corn, theories,
 Africa, 7, 8
 American, 8, 9
 Asiatic, 7
 divergent evolution, 14, 17
 Herbalists, 6
 Hybrid, 11, 17
Oryzaephilus surinamensis, 598
 Overdominance, 266, 267
Oxalis, 507, 509

P

Pantothenic acid, 645, 659
 Parthenogenetic diploids, 26
 Pellagra, 646
 Penicillium ear rot, 491
Penicillium oxalicum, 469, 473
Peregrinis maidis, 521, 592, 595
Phaeogenes nigridens, 569
 Phosphorus fertilization, 354
 Phosphorus percentage,
 in leaves, 296, 304, 307
 in stem, 297
 in whole plant, 299, 301
Phyllophaga fusca, 552
 hirticula, 552
 rugosa, 552
 tristis, 552
Phyllophaga spp., 275, 500
Physalospora zeae, 488
Physalospora zeicola, 490
 Physiological maturity, seed, 395
Physoderma zeae-maydis, 511
Phytomonas lapsa, 482
Phytomonas stewartii, 456
 Picker losses, 398
 Picking seed corn, 397
 Pink corn worm, 601
 Planter plates, 410
 Planting depth, 360
 Planting methods,
 bedding, 359
 listing, 359
 surface planting, 358
 Planting rate, 360, 684
 Planting seed fields, 385
 Planting, time of, 359
Plodia interpunctella, 600
 Pod corn, 12, 111
 Pollen, fossil, 13, 53
 Pollination, 103
 Polyploidy, 23, 131
Polytoca barbata, 18
 Popcorn, 423-439
 cross sterility, 435, 436
 drying, 429
 hybrids, 433
 mass selection, 432
 origin of, 423
 production and utilization, 437, 438
 refrigeration, 430

storage, 430

varieties, 424

Jap Hulless, 424

Queen Golden, 424

South American, 425

Spanish, 425

Supergold, 425

White Rice, 424

Pop-dent recoveries, 436

Popillia japonica, 591

Popping expansion,

 effect of age on, 431

 effects of xenia, 431

 inheritance of, 431

 methods of testing, 427

 moisture content, 427

Potassium fertilization, 354

Potassium percentage,

 in leaves, 296, 303, 307

 in stem, 297

 in whole plant, 299, 301

Preferential segregation, 198

Protein deficiency, 637

Protein quality, 643

Protein quantity, 642

Pseudaletia unipuncta, 578

Pseudomonas alboprecipitans, 513

Pseudomonas syringae, 515

Puccinia polysora, 510

Puccinia sorghi, 278, 507, 509

Pure line method, 233

Purple sheath spot, 514

Pyrausta nubilalis, 272, 564

Pyroderces rileyi, 601

Pythium aphanidermatum, 479

Pythium arrhenomanes, 481

Pythium butleri, 479

Pythium debaryanum, 481

Pythium graminicolum, 481

Pythium root rot, 481

Pythium spp., 276, 413, 469

Pythium stalk rot, 479

R

Radioactive isotopes, 306

Rainfall distribution and yield, 328, 329

Recurrent selection, 257, 259

 general combining ability, 260

 reciprocal recurrent selection, 262

 specific combining ability, 261

Relatives of corn,
 teosinte, 9
 tripsacum, 9
Rhizoctonia ear rot, 413, 491
Rhizoctonia zeae, 491
Rhopalosiphum maidis, 587
Rhopalosiphum prunifolae, 595
 Riboflavin, 645, 655
 Rice weevil, 595
 chemical control, 597
 habits and biology, 596
 varietal resistance, 597
 Ring chromosomes, 132, 195
 Rootworm, corn, 539
 chemical control, 543
 habits and biology, 540
 varietal resistance, 542
 southern, 544
 chemical control, 546
 cultural practices, 546
 habits and biology, 545
 varietal resistance, 545
 Row ratio in seed fields, 384

S

Saccharification, 630
 Saccharum, 524
Saccharum officinarum, 18
 Sales methods, 417
 Sampling field run seed, 400
Schistocerca americana, 585
Schlerachne punctata, 18
Sclerospora graminicola, 523
 macrospora, 524
Sclerotium bataticola, 471
 Screen arrangements for sizing, 406, 407
 Seed and seedling diseases, 469
 Seedbed preparation, 356
 Seed cleaning, 405
 Seed corn, drier, 402
 drying, 401
 shelling, 404
 sizes, 408
 sizing, 405
 sorting, 400
 storage, 414, 416
 Seed corn beetles, 558
 Seed corn maggot, 555
 Seed drying equipment, 402
 Seed growers, 379
 Seed plate suggestions, 409
 Seed sales methods, 417
 Seed stock increase, 382
 Seed viability, tetrazolium, 414
 Seeds, sampling, 400
 sorting, 400
 storage, 414
 treatment, 410
 unloading, 400
 Seed weighing and bagging, 411
 Selection for yield, 243
Setaria lutescens, 514
Setaria viridis, 524
 Silicon in leaf tissue, 305, 307, 310
 Single cross seed production, 382
Sitophilus granarius, 597
Sitophilus oryza, 595
Sitotroga cerealella, 599
 Smut, corn, 278, 517
 Soap stock, 625
 Sod webworms, 551
 Soft corn, 640
 Soil fertility and seed production, 384
 Soil insects, 539
 Soil protection practices, 345
 parallel strips, 346
 terracing, 346
 Soil requirements for corn production, 344
 Soil structure, 347, 349
Sorghum dimidiatum, 18
 halepense, 18, 27
 intrans, 18
 purpureo-sericeum, 18
 randolpheanum, 18
 sudanensis, 27
 versicolor, 18
 vulgare, 18
Spacelotheca reiliana, 278, 519
 Specific combining ability, 248, 261, 433
 Spikelet, female, 90
 male, 89
 Sprays, postemergence, 366
 pre-emergence, 366
 Stalk borer, lesser, 580
 Starch, 618
 dextrins and British gums, 620
 hydrolytic products, 622
 thick boiling, 619
 thin boiling, 620
 Starch-gluten separation, 617

- Steep water, 617, 626
 Steeping corn, 615
Stenobothrus, 154
 Storage of seed corn, 414, 416
 Stored grain insects, control of, 374, 601
 Sugar-cane beetle, 556
 Sugar-cane mosaic, 520
 Sweet-corn, 441-461
 breeding, 450
 chemical composition, 453
 culture, 445
 fertilizers, 445
 harvesting, 448, 449
 planting, 447
 spacing, 446
 tellerling, 447
 drought resistance, 457
 hybrids, 460-461
 kernel color, 457
 moisture percentage at harvest, 448
 quality,
 flavor, 453
 tenderness, 450
 resistance to disease, 456
 to insects, 456-457
 seed production, 458, 459, 460
 silk color, 457
 uses, 443-445
 canning, 443
 drying, 445
 freezing, 444
 market corn, 444
 varieties,
 Black Mexican, 442
 Egyptian, 442
 Narrow Grain Evergreen, 451
 Stowell Evergreen, 454
 yield, 455
Sympeisis viridula, 569
 Synapsis, 142
 corn $\times$ teosinte hybrids, 29, 30, 31
 multivalent, 25
 Synthetics, 254
 Syrup, corn, 623
- T**
- Tenebroides mauritanicus*, 598
 Teopod, 112
 Tetraploids, 133, 134
 Tetrazolium, measure of seed viability, 414
 Thiamine, 655
 Thrips, 592
 Tillage, deep, 347
Toxoptera graminum, 521
 Translocations, A-B chromosomes, 176
 reciprocal, 130, 147, 152, 160, 169
 alternate and adjacent segregations in, 173
 homologous pairing in, 180
Trichoderma sp., 413
Trigonotylus brevipes, 592
Trillium sp., 154
Trilobium castaneum, 599
 confusum, 599
 Triploids, 133
 Tripsacum, apomixis, 13
 chromosomal variations, 13
 chromosome knobs, 22, 129
 hybrids, 24
 polyembryony, 13
 polyploidy in, 23
 species,
 Tripsacum australe, 18
 dactyloides, 11, 18, 34, 36, 108
 floridanum, 18, 28, 34, 36
 latifolium, 18
 laxum, 18
 maizar, 18, 24, 37
 pilosum, 18
 zopilotense, 18, 24, 37
 Trisomes,
 primary, 135, 136
 secondary, 135, 137
 tertiary, 135, 138
 Tryptophan, 281, 644, 645, 647
Typhaea stercorea, 601
- U**
- Ustilago maydis*, 278, 517
- V**
- Valine, 281, 644
 Varietal hybridization, 225
 Vascular bundles,
 histogenesis, 77
 Vegetative morphology,
 epidermis, 85

leaf, 84
root, 81
stem, 75
vascular bundles, 77, 82, 85
Virus diseases, 520, 594
 corn mosaic, 520
 corn stunt, 521
 leaf fleck, 522
 sugar cane mosaic, 520
Vitamin A, 637, 651, 653
Vitamin B₁₂, 645
Vitamin E, 637
Vivipary, 111

W

Waxy corn, 7, 621
Waxy starch, 621
Weather and plant growth, 318
 emergence to tasseling, 321
 maturity, 324
 planting to emergence, 318
 tasseling and silking, 323
Weather and yield, 325, 335
 relation to calendar periods, 326

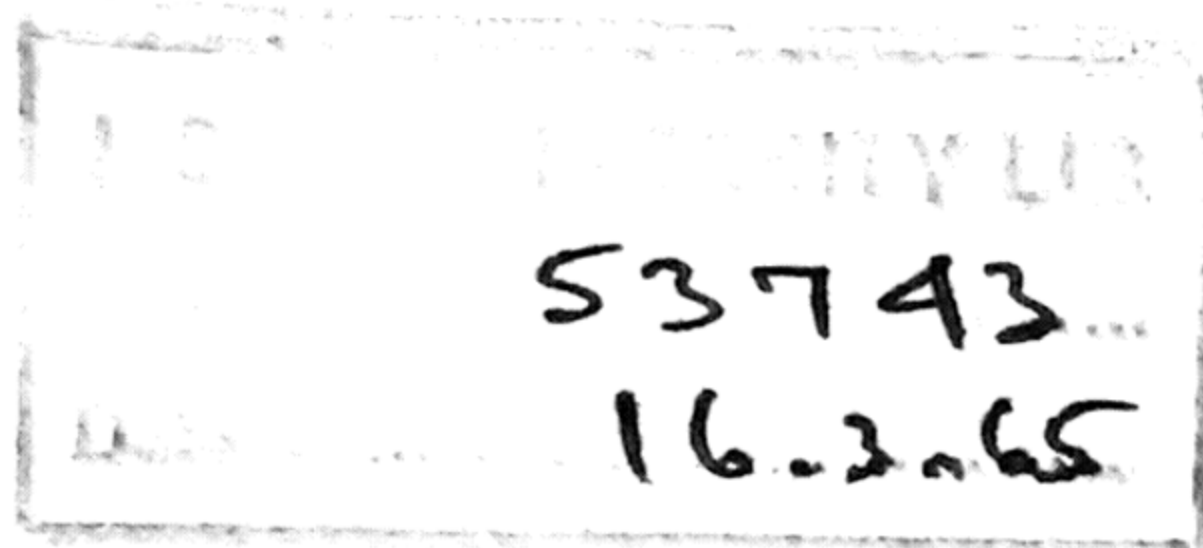
 stage of crop development, 333
Webworms, sod, 551
Wet milling, 613
 flow chart, 615
White grubs, 552
 control, 554
 habits and biology, 553
Wireworms, 548
 cultural practices, 549

Y

Yellow vs. white corn, 652
Yield, effect of rainfall and temperature
 on, 325-335
Yield and other weather factors,
 evapotranspiration, 335
 hail, 335
 humidity, 338
 radiation, 338

Z

Zein, 281, 626, 644
Zonate leaf spot, 515



ALLAMA IQBAL LIBRARY



53743